

Taxonomy and redescription of the Swamp Antechinus, *Antechinus minimus* (É. Geoffroy) (Marsupialia: Dasyuridae)

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ABSTRACT

We provide a taxonomic redescription of the dasyurid marsupial Swamp Antechinus, *Antechinus minimus* (Geoffroy, 1803). In the past, *A. minimus* has been classified as two subspecies: the nominate *A. minimus minimus* (Geoffroy, 1803), which is found throughout much of Tasmania (including southern Bass Strait islands) and *A. minimus maritimus* (Finlayson, 1958), which is found on mainland Australia (as well as some near-coastal islands) and is patchily distributed in mostly coastal areas between South Gippsland (Victoria) and Robe (South Australia). Based on an assessment of morphology and DNA, we conclude that *A. minimus* is both distinctly different from all extant congeners and that the two existing subspecies of Swamp Antechinus are appropriately taxonomically characterised. In our genetic phylogenies, the Swamp Antechinus was monophyletic with respect to all 14 known extant congeners; moreover, *A. minimus* was well-positioned in a large clade, together with all four species in the Dusky Antechinus complex, to the exclusion of all other antechinus. Within *A. minimus*, between subspecies there were subtle morphological differences (*A. m. maritimus* skulls tend to be broader, with larger molar teeth, than *A. m. minimus*, but these differences were not significant); there was distinct, but only moderately deep genetic differences (3.9–4.5% at mtDNA) between *A. minimus* subspecies. Comparatively, across Bass Strait, the two subspecies of *A. minimus* are morphologically and genetically markedly less divergent than recently recognised species pairs within the Dusky Antechinus complex, found in Victoria (*A. mimetes*) and Tasmania (*A. swainsonii*) (9.4–11.6% divergent at mtDNA). □ *Marsupialia*, *Dasyuridae*, *dasyurid*, *carnivorous marsupial*, *Australia*.

In 1803, Étienne Geoffroy Saint-Hilaire, a French naturalist colleague of Lamarck, described a new carnivorous marsupial that had been collected by Peron from Tasmania. Geoffroy dubbed his new species *minimus*, placing it within the genus

Dasyurus that already contained three species, two of which were quolls; thus, the epithet *minimus*, meaning small, was appropriate for the time. Compared to the other 14 extant species of antechinus known today, *A. minimus* is in fact

medium-large in size, but it was to be another 35 years after Geoffroy coined *minimus* before a second antechinus was even discovered, by Waterhouse (*A. flavipes* [then *Phascogale*] in 1838), followed quickly by a third, *A. swainsonii* (Waterhouse 1840). The genus *Antechinus* was duly erected by Macleay in 1841, after the discovery of a fourth species, *A. stuartii*. More than 60 years later, there followed two further new species, named by renowned English taxonomist Oldfield Thomas (*bellus* in 1904 and *godmani* in 1923). No other species was named under *Antechinus* until Van Dyck's *leo* in 1980. In the decades that followed, the advent of molecular techniques allowed resolution of numerous cryptic taxa across many groups of organisms, including mammals. Pioneering genetic studies examined relationships among dasyurid genera (e.g., Armstrong *et al.* 1998; Baverstock *et al.* 1982; Krajewski *et al.* 1997) prompting description of other antechinus species (*agilis* by Dickman *et al.*, 1998, *subtropicus* and *adustus* [the latter raised from subspecies of *stuartii*] by Van Dyck & Crowther, 2000). So by the time of Van Dyck's (2002) morphological review, there were ten extant species of antechinus: Swamp Antechinus, *A. minimus* (Geoffroy); Yellow-footed Antechinus, *A. flavipes* (Waterhouse); Brown Antechinus, *A. stuartii* Macleay; Dusky Antechinus, *A. swainsonii* (Waterhouse); Fawn Antechinus, *A. bellus* (Thomas); Rusty Antechinus, *A. adustus* (Thomas); Atherton Antechinus, *A. godmani* (Thomas); Cinnamon Antechinus, *A. leo* Van Dyck; Agile Antechinus, *A. agilis* Dickman, Parnaby, Crowther and King and Subtropical Antechinus, *A. subtropicus* Van Dyck and Crowther. But in the years that followed Van Dyck's review, it became clear from aberrant specimens held in museum collections that other antechinus species lay waiting to be described.

To investigate this cryptic variation, three years ago our research group began a systematic and taxonomic revision of the extant members of the genus, which resulted in description of five new species of antechinus (see Baker, Mutton & Hines 2013; Baker, Mutton, Hines & Van Dyck 2014; Baker, Mutton, Mason & Gray 2015; Baker, Mutton & Van Dyck 2012) and redescription of

several others (Baker & Van Dyck 2012, 2013a,b). The new species description sequence ran as follows. First, Baker, Mutton & Van Dyck (2012) diagnosed an eleventh species, the Buff-footed Antechinus *A. mysticus*, found sheltering under the taxonomic umbrella of the ubiquitous Yellow-footed Antechinus, *A. flavipes*. Then, in the process of investigating the distributional range of *A. mysticus* between south-east and mid-east Queensland, Baker, Mutton & Hines (2013) stumbled across a twelfth antechinus species, the Silver-headed Antechinus, *A. argentus*, which is apparently restricted in distribution to just a few square kilometres, on the escarpment of Kroombit Tops NP in south-east Queensland. At about the time of discovering *A. argentus*, we shifted focus within the genus to the Dusky Antechinus, *Antechinus swainsonii*. The thirteenth species of Antechinus, the likely endangered *A. arktos*, was raised after comparison of northern outlying Dusky Antechinus populations with other mainland *A. s. mimetes* (Baker, Mutton, Hines & Van Dyck 2014). But after genetically screening some newly acquired tissue samples of Tasmanian *A. swainsonii*, it became clear there were further cryptic species within the Dusky Antechinus group. Our research group subsequently undertook a more comprehensive morphological and genetic review of Dusky Antechinus, duly naming a new (likely threatened) species apparently restricted to Tasman Peninsula, *A. vandycki*, and transferring the two mainland subspecies of *A. swainsonii* (*mimetes* and *insulanus*) to subspecies within the raised *A. mimetes* (Baker, Mutton, Mason & Gray 2015). This research indicated deep divergence between species on either side of Bass Strait, with *A. mimetes* (Vic, NSW) being about 10% divergent to both Tasmanian species: *A. swainsonii* and *A. vandycki*. Since the Swamp Antechinus, *A. minimus*, has a similar distribution to southern Dusky Antechinus, on either side of Bass Strait, with subspecies *maritimus* on the coastal mainland (SA, Vic and neighbouring islands) and subspecies *minimus* on Tasmania (and southern Bass Strait islands), we were prompted to investigate if there were also cryptic taxa hiding under *A. minimus*.

A. minimus (Geoffroy 1803) has an interesting taxonomic history. Although the original date of publication of this species was given as '1803...December (fide Sherbon)' by Iredale and Troughton (1934), they cited the page reference as p. 159 in the *Bulletin des Sciences par La Société Philomathique de Paris* No. 81. Tate (1947) did the same. This was later corrected to p. 259 (by Mahoney & Ride 1988), but relatively recently it was proposed that the species' publication date be amended to 1904 in favour of a subsequent, expanded description in the *Annales du Muséum d'Histoire Naturelle* (Julien-Laferrrière 1994). This amendment is most likely invalid.

Furthermore, the veracity of the *A. minimus* type locality received attention from Wakefield and Warneke (1963) who noted that Waterhouse's (1846) reference to Maria Island (near Hobart) as the type locality conflicted with Geoffroy's (1803) original statement that the holotype had come from an island found in Bass Strait. According to Wakefield and Warneke (1963), the confusion arose from an account by Péron (1807) of a single 'Dasyure' collected on Maria Island. The identity of this animal, Wakefield and Warneke argued, had confused Péron at the time as much as the description of events had later confused Waterhouse. The 'dasyure' was finally correctly identified and ended up being described as the holotype of the Eastern Pygmy-possum *Cercartetus nanus* (Desmarest, 1818). Thus, the only likely type locality attributable to *A. minimus* was eventually identified as (ironically) Waterhouse Island, a tiny (287 hectare) island located just 3 km off the north-eastern coast of Tasmania.

Unfortunately, further confusion followed, three years after the description of *A. swainsonii* (Waterhouse 1840), Waterhouse (1841: 142), deferring to the judgement of Gould, merged *swainsonii* under *minimus* 'I have altered the name I had applied to it, of *swainsonii* into *minima*, Mr. Gould, who has recently examined the original of Geoffroy's *Dasyurus minimus*, having informed me that that animal was specifically identical with the *swainsonii*. Geoffroy's specimen must be young, being only four French inches in length'. It was another

three years before Waterhouse was able to examine the *D. minimus* holotype himself and thereafter re-establish *swainsonii*, writing 'Mr. Gould imagined this species was identical with the *Dasyurus minimus* of Geoffroy; I have recently compared the two animals together, and find this is not the case. The skull of *P. swainsonii* is proportionately narrower...' (Waterhouse 1846: 412). Waterhouse must have been reasonably confident of his skills of external comparative assessment, since the skull of the *A. minimus* holotype was not removed from the mount until 1937 (Tate 1947)!

A. minimus was not knowingly collected from mainland Australia until 1962. However, Finlayson (1958) had encountered it earlier in South Australia and, mistaking it for a distinct form of *A. swainsonii*, named it *Plascogale (Antechinus) swainsonii maritima* from Port MacDonnell (collected in June, 1938). But Wakefield and Warneke (1963) noted Finlayson's error and referred *maritimus* to *A. minimus*.

Early genetic work addressed the distinctiveness of mainland and Tasmanian subspecies of *A. minimus* and *A. swainsonii*. Smith (1983) examined electrophoretic variation in *A. minimus* and *A. swainsonii* on either side of Bass Strait and concluded that respective mean genetic distances of 0.035 ± 0.009 and 0.085 ± 0.015 suggested that subspecies status was warranted in *A. minimus* and at least subspecies status was warranted for *A. swainsonii*. The sampling of *A. minimus* in Smith's study included a couple of Tasmanian populations: Flinders Island in the north and Bruny Island in the south, compared to four populations on the mainland (Vic): Gembrook, Dartmoor, Cape Liptrap and Cape Otway. Given that Smith's suspicions of deeper variation between *A. swainsonii* subspecies was recently born out by species level differences being attributed to these Dusky Antechinus populations after detailed morphological and comparative genetic assessment (see Baker, Mutton, Mason & Gray 2015), we were intrigued to investigate in more detail the comparative situation in *A. minimus*. Here, we report the results of this work.

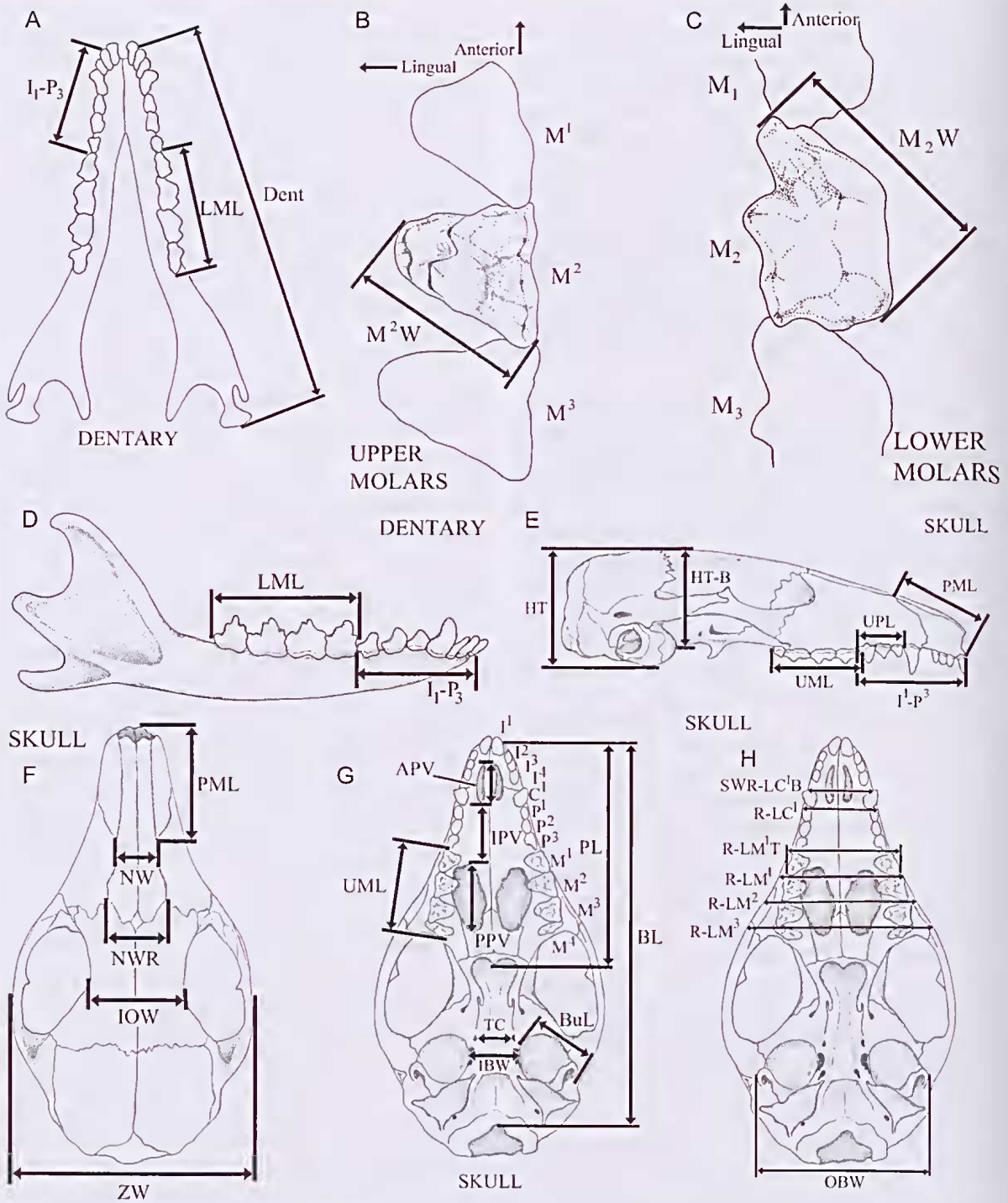


FIG. 1. A guide to measurement of variables: skull and dentary (A-H), and external body measures opposite page (I, J).

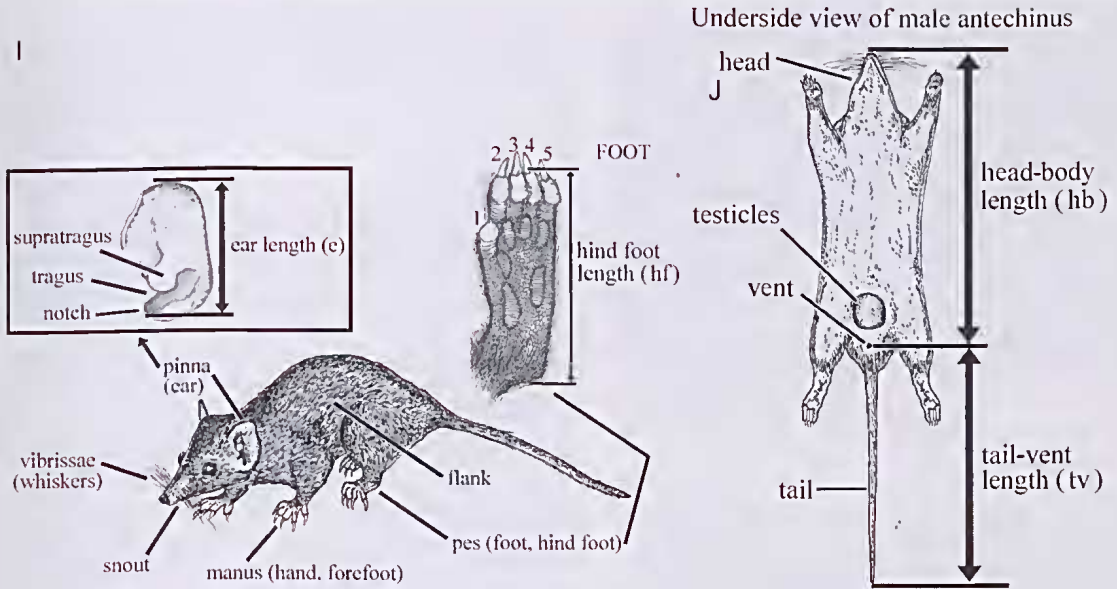


FIG. 1. Continued ...

METHODS

Analyses of morphological data

Figure 1 describes and depicts the 30 skull and dental, and 5 external measurements taken. Measurements were made using Mitutoyo CD-8CSX digital calipers (taken to the nearest 0.0 X mm). Age variation was minimised by using only animals which possessed fully erupted permanent P³ teeth and thus deemed to be adult. Tooth nomenclature follows Archer (1974) and basicranial nomenclature follows Archer (1976). Colour nomenclature used in the holotype pelage description follows Ridgway (1912).

Measured variables are as follows (and see Fig 1): wt = body weight (grams); hb = head-body length (mm) from tip of nose to mid-vent; tv = tail-vent length (mm) from mid-vent to tip of tail proper (excluding hair at tip); hf = hind foot length (mm) from behind heel to tip of longest extended toe (excluding claw); e = ear length (mm) from extended ear tip to notch at rear base of tragus; APV = maximum anterior palatal vacuity length; BL = basicranial skull length, excluding incisors; Dent = dentary length, excluding incisors; IBW = minimum

width between auditory bullae; LOW = minimum width of interorbital constriction; IPV = minimum interpalatal vacuity distance; M²W = maximum width of upper molar 2 measured diagonally from anterior lingual to posterior labial points; NW = width of nasals at the nasal / premaxilla / maxilla junction; OBW = basicranial width from outside right and left auditory bullae; PPV = maximum posterior palatal vacuity length; R-LC¹ = skull width level with the posterior of upper canines; R-LM¹ = skull width level with the junction of the first and second upper molars; R-LM¹T = maximum width between the ectolophs of the left and right first upper molars; R-LM² = skull width level with the junction of the second and third upper molars; R-LM³ = skull width level with the junction of the third and fourth upper molars; ZW = maximum zygomatic width; HT = skull height; PL = length of palate; SWR-LC¹B = skull width level with the anterior of upper canines; TC = minimum distance separating transverse canals; NWR = width of nasals at the nasal / maxilla / frontal junction; PML = length of premaxilla; UML = maximum length of upper molar row, M¹-M⁴; HT-B = skull height measured immediately anterior of auditory bullae; BuL = auditory bulla length; I¹-P³ = crown length from anterior edge



FIG. 2. *Anitechinus minimus minimus* holotype mount of MNHN C.G. 1987-233; No. 381; Type No. 628

of upper incisor 1 to posterior edge of upper premolar 3; LML = maximum length of lower molar row, M_1 - M_4 ; I_1 - P_3 = crown length from anterior of lower incisor 1 to posterior of lower premolar 3; M_2W = maximum width of lower molar 2 measured diagonally from anterior lingual to posterior labial points; UPL = crown length of upper premolar row, P^1 - P^3 .

Species clades returned from constructed DNA-based phylogenies (see below) matched to voucher specimens were used as testable hypotheses in subsequent morphological analyses; thus, multivariate analyses enabled us to predict membership of individuals in hypothesised species groups based on a combination of skull morphology variables, whereas univariate ANOVAS (and subsequent post-hoc tests) for each variable enabled us to test for significant variation within each variable and determine which variables differed for comparisons of our putative *A. minimus minimus* with each other putative species pair. The combination of univariate and multivariate analyses was essential to permit both fine-scale pairwise comparisons demonstrating species by species differences to facilitate best-practice species management for the future and also broadscale comparisons among all species within both *A. minimus* and the closely related Dusky Antechinus complex, to best illustrate broader differences across all measured variables.

Statistical analyses of morphometrics were undertaken using the program STATISTICA

Version 7 (Statsoft Inc. 2004). Samples were initially tested for normality with the Kolmogorov-Smirnov and Lilliefors tests and homogeneity of sample variances using Levene's test. Analysis of Variance (ANOVA) was used to analyse variation in means among all putative antechinus species, tested under separate hypotheses for each measured external and cranial/dentition variable. In each ANOVA, Post-hoc Unequal N HSD tests (a modification of Tukey's HSD) were used to test pairwise differences (at $P < 0.05$) in external variables and craniodental measures between *A. minimus minimus* and each proposed congener, to compensate for potential Type 1 errors, and since sample sizes differed between species. Multivariate analyses were conducted to optimise dimensionality of each variable set and maximise relationships between variable sets. Discriminant Function Analysis (DFA) was used to determine assignment reliability within proposed species groupings and subsequent Canonical Variate Analysis (CVA) generated independent functions that best discriminated between the putative species.

Baker, Mutton, Mason and Gray (2015) recognised the close genetic relationship between *A. minimus* and all members of the Dusky Antechinus complex, indicating that these taxa formed a combined well-supported clade to the exclusion of all congeners. Thus, univariate statistics (means, standard deviations, range minima and maxima) were compiled for each of the external and internal (cranial/dental) measures for Swamp Antechinus, *A. minimus minimus* and *A. minimus maritimus* as well as the four species (5 taxa) within the dusky antechinus species complex: Tasmanian Dusky Antechinus, *A. swainsonii*; Tasman Peninsula Dusky Antechinus, *A. vaudycki*; Mainland Dusky Antechinus, *A. mimetes mimetes*, *A. mimetes insulauus*; and Black-tailed Dusky Antechinus, *A. arktos*. A range of scatterplots were constructed to show the main discriminating variable pairs among these species. *Antechinus minimus* and all members of the Dusky Antechinus complex are strikingly different in both size and morphology to all congeners, so no other species were included

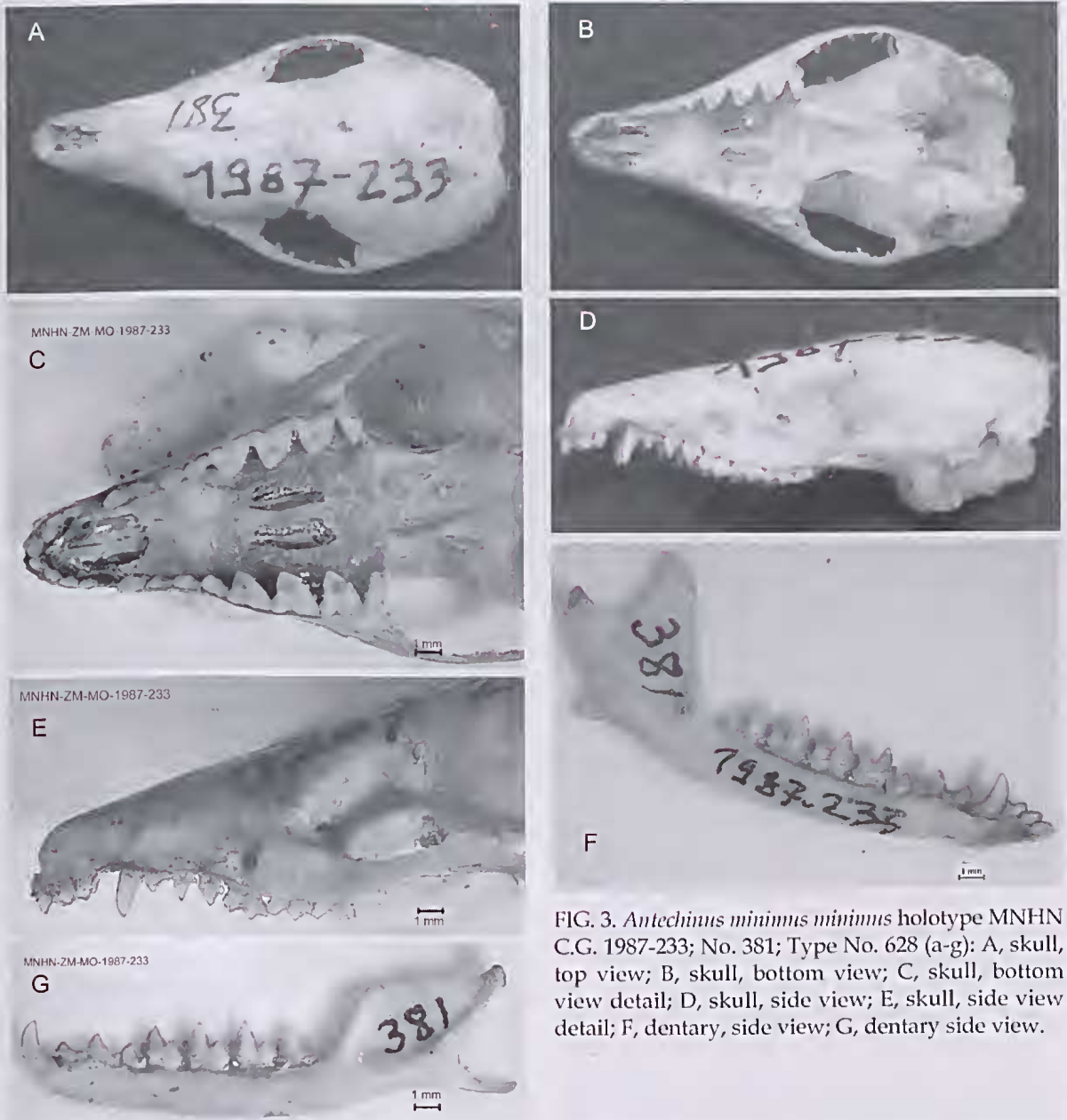


FIG. 3. *Antechinus minimus minimus* holotype MNHN C.G. 1987-233; No. 381; Type No. 628 (a-g): A, skull, top view; B, skull, bottom view; C, skull, bottom view detail; D, skull, side view; E, skull, side view detail; F, dentary, side view; G, dentary side view.

for these comparisons. DFA and CVA were conducted for *A. minimus minimus* and *A. minimus maritimus*, as well as the four species (5 taxa) within the Dusky Antechinus species complex. External body measures, while included in univariate analyses, were excluded from multivariate analyses because of missing data (numerous museum specimens included

only skull material for the registered specimen) - this served to maximise the number of individuals of each species used in any given multivariate analysis. Antechinuses are known to be sexually dimorphic in size (Marlow 1961; Soderquist 1995; Williams & Williams 1982), so sexes were analysed separately for all measured variables.

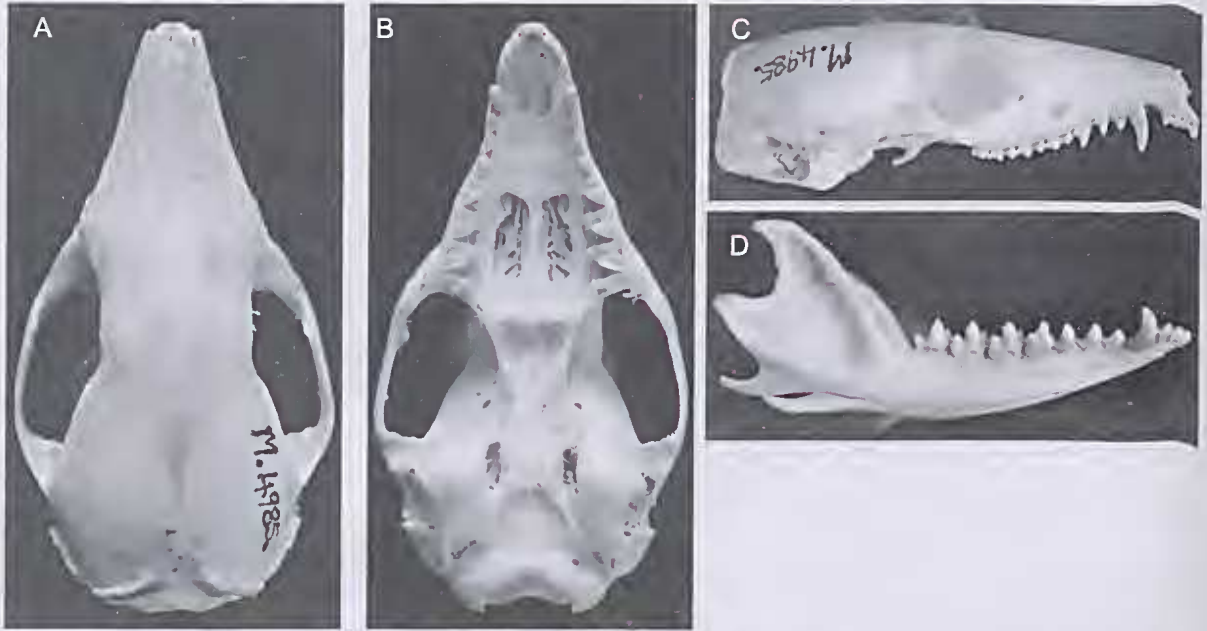


FIG. 4. *Antechinus minimus maritimus* holotype SAM M4985 (a-d): A, skull, top view; B, skull, bottom view; C, skull, side view; D, dentary, side view.

Analyses of Genetic Data.

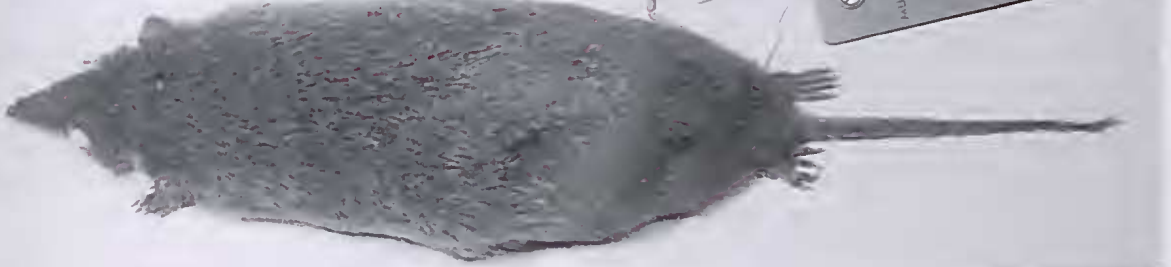
Comprehensive examination of genetic structuring in the genus *Antechinus* is the subject of an ongoing parallel research project and as such will not be presented in detail here. However, for the purpose of postulating DNA-based species groups that were matched with vouchers and subsequently tested with a comprehensive morphological data set, we present the preliminary DNA-based phylogenies for all recognised extant antechinus species, as well as DNA uncorrected percentage divergence ranges between each existing species paired with *A. minimus minimus* (see results). A portion (607 bp) of the mitochondrial Cytochrome B gene (CytB) and a portion (699bp) of the nuclear Interphotoreceptor Binding Protein gene (IRBP) were targeted using primers as described in Mutton (2011). Sequences were aligned by eye using Bioedit Version 7.1.11 (Hall 1999). Bayesian phylogenies (using mtDNA alone and also a concatenated dataset partitioned as mtDNA and nDNA) were reconstructed using MrBayes Version 3.2.1 (Ronquist & Huelsenbeck 2003) under the General Time

Reversible Model of sequence evolution as determined by MrModelTest 2.3 (Nylander, 2004), incorporating invariant sites and a gamma shape distribution of 2; in MrBayes, tree search was run for 10 million generations with a 25% burnin, as recommended by program guidelines. Resulting phylogenies were output in the program Treeview (Page, 1996). A p-distance matrix was output based on aligned sequences in MEGA 6 (Tamura *et al.* 2013) and % divergences calculated by multiplying each value by 100; % divergence ranges incorporating minima and maxima were generated for each putative species pair.

Abbreviations used for Institutions housing specimens examined in this study are as follows: QM – Queensland Museum, Brisbane, Queensland, Australia; QVM – Queen Victoria Museum, Launceston, Tasmania, Australia; MTAS – Tasmanian Museum and Art Gallery, Hobart, Tasmania, Australia; MVIC – Museum Victoria, Melbourne, Victoria, Australia; BMNH – British Museum Natural History, London, England; MNHN – Muséum National D’Histoire

Swamp Antechinus, *Antechinus minimus* (É. Geoffroy)

A



B

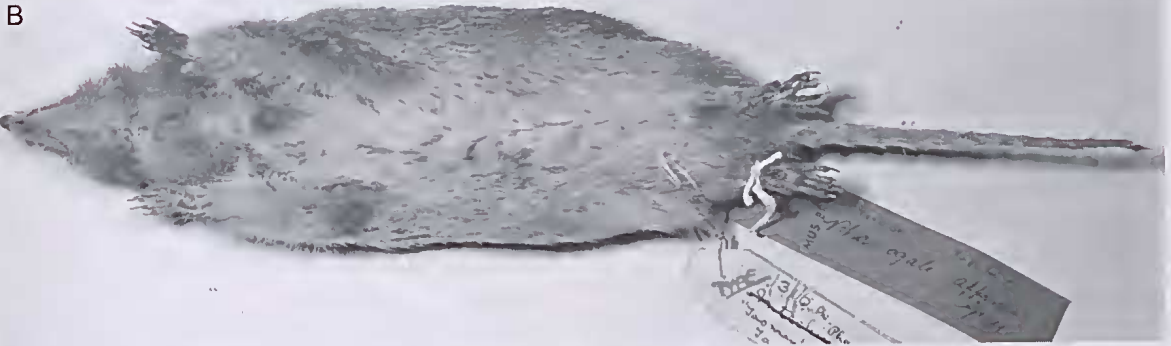


FIG. 5. *Phascogale affinis* syntype study skin BMNH 41.1241 (a-b): A, above; B, below.

Naturelle, Paris, France; SAM - South Australian Museum, Adelaide, Australia.

RESULTS

We provide below detailed holotype descriptions of *Antechinus minimus minimus* and *A. m. maritimus*, neither of which has been adequately described in the past.

Systematics

Antechinus minimus (É. Geoffroy, 1803)

Dasyurus minimus Geoffroy, 1803

Phascogale affinis Gray, 1841

Material examined. Holotype. MNHN (Muséum National D'Histoire Naturelle, Paris), Catalogue Général No. C.G. 1987-233; Nouveau Catalogue de

la Galerie Zoologie No. 381; Type No. 628 (refer Figs 2-3). Collected by F. Peron.

Adult male, faded ('...the little animal described by Geoffroy has been exposed to the action of light in a museum for upwards of forty years, we cannot but suppose its colouring has changed' Waterhouse, 1846) mount and skull, No. 192A, with basicranium smashed, lower dentary separated at LC₁ and LA ramus missing ('the hinder part of the palate is mutilated', Waterhouse, 1841), and both in poor condition (notwithstanding recent reassurances from the French... 'Montage en bon état sauf yeux absents. Crâne en bon état' [Julien-Laferrrière, 1994: 7]).

Type Locality. Waterhouse Island, Bass Strait, Tasmania, c. 40°40'S 148°10'E. Altitude not supplied.

Rediagnosis. There are no significant morphological differences between *A. minimus minimus* and *A. minimus maritimus*. However, *A. minimus minimus* differs from *A. minimus maritimus* in having a typically narrower skull at a point level with the molar teeth and often

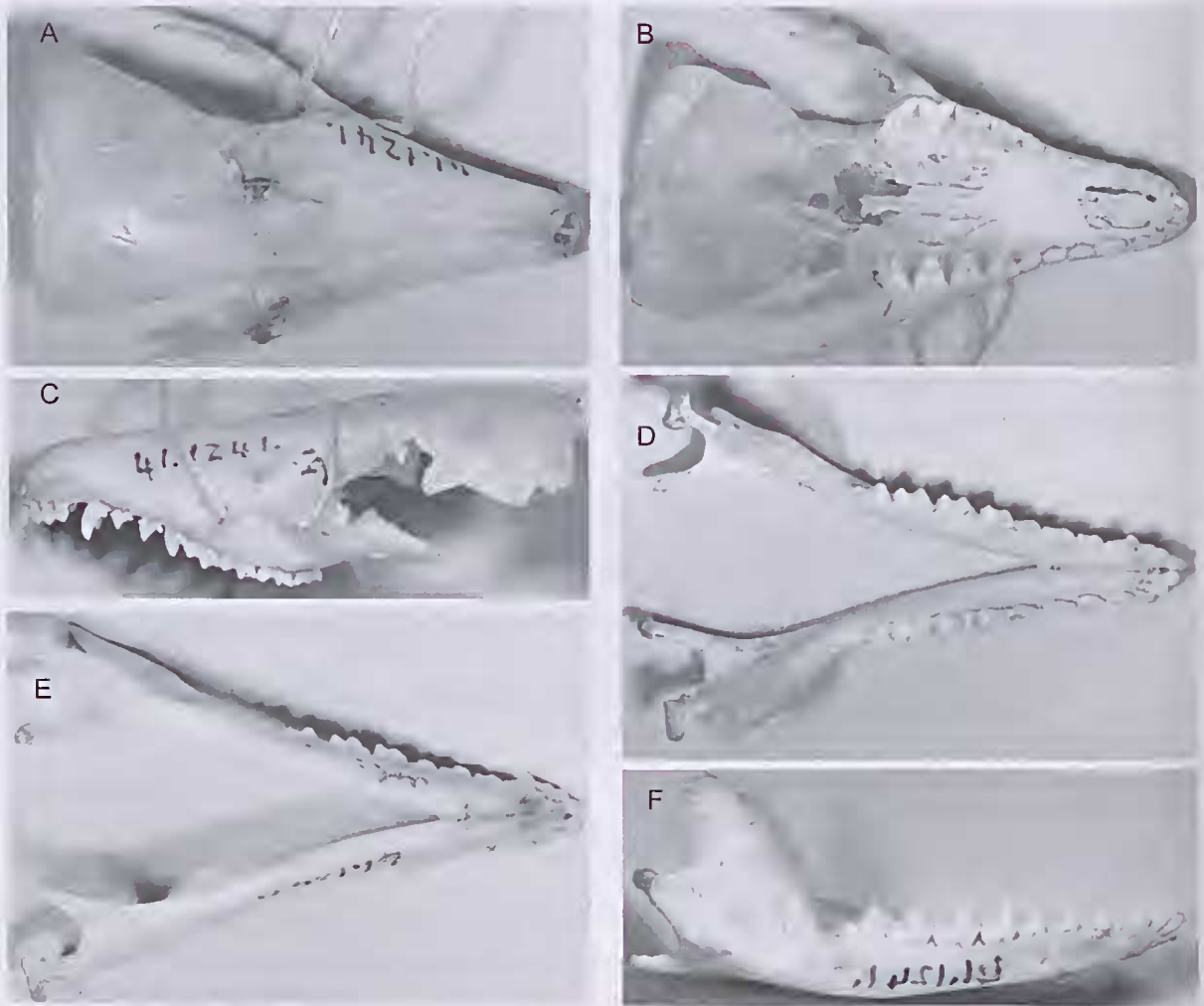


FIG. 6. *Phascogale affinis* syntype BMNH 41.1241 (a-f): A, skull, top view; B, skull, bottom view; C, skull, side view; D, dentary, top view; E, dentary, bottom view; F, dentary, side view.

smaller upper and lower second molar teeth. *Antechinus minimus minimus* also tends to have a longer tail and larger feet than *A. minimus maritimus*. *Antechinus minimus minimus* differs from all members of the Dusky Antechinus complex in having a leaden grey head merging to yellowish (rather than brownish) rump. Also, *A. minimus minimus* tends to have a heavier rump and shorter tail relative to body length compared to all members of the Dusky Antechinus complex. *Antechinus minimus minimus* is easily distinguished from all other antechinus species, being notably

larger, heavier bodied, relatively shorter tailed (compared to head-body length) and smaller-eared; also, the snout is relatively longer/narrower with relatively long anterior palatal vacuities compared to most other antechinus species outside the Dusky Antechinus complex.

Description. Holotype. *Pelage.* The skin of the mounted holotype is so faded that a formal pelage description will not be presented here. Nevertheless, the mount shows a definite warming of dorsal fur from head to rump and flanks. The skin of the better preserved *A. affinis* is described in detail under SYNONYMS.

Swamp Antechinus, *Antechinus minimus* (È. Geoffroy)

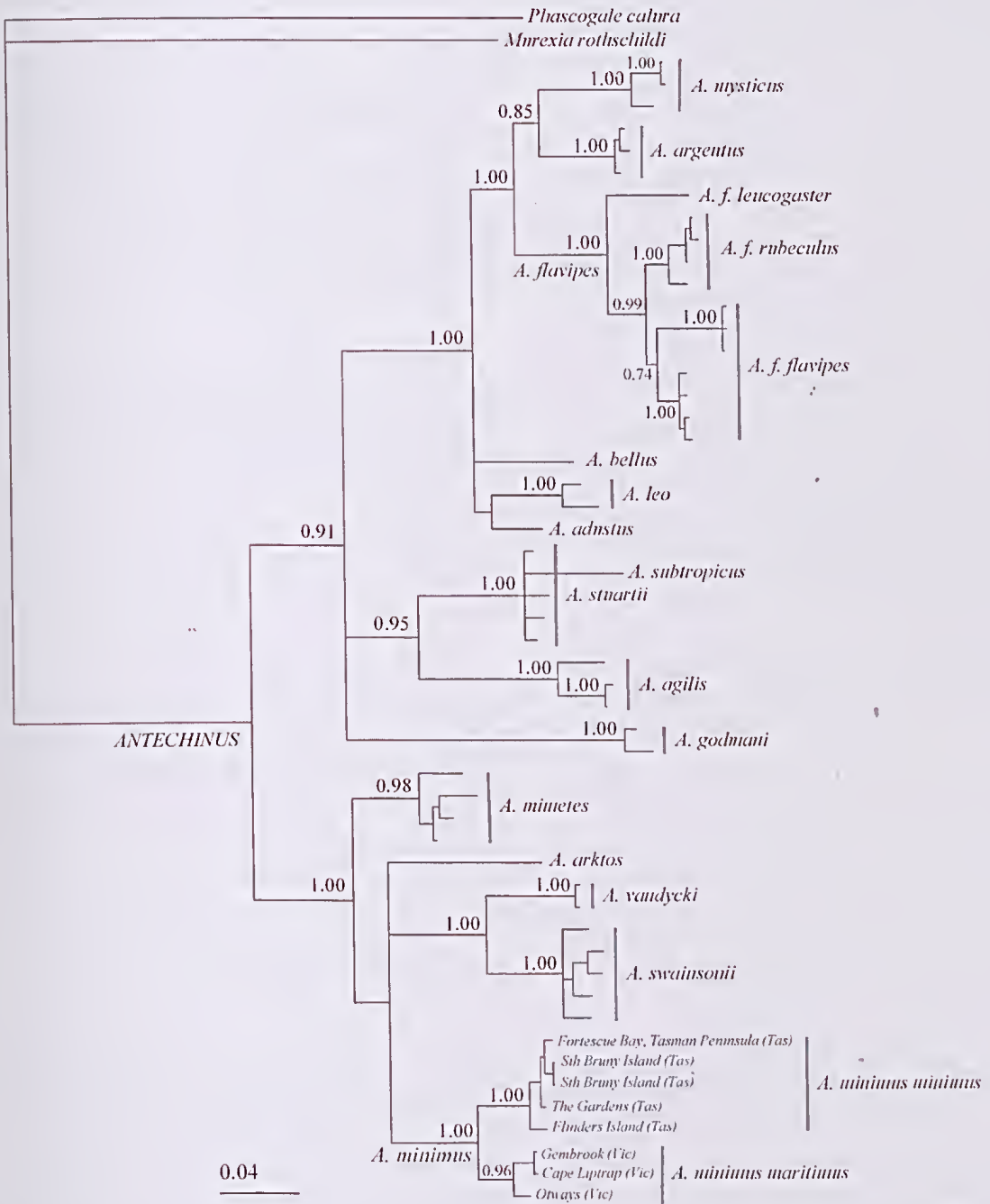


FIG. 7. Bayesian phylogeny of the genus *Antechinus* based on mitochondrial (Cytb) gene sequences. Posterior probabilities are shown at each node (those less than 0.70 are omitted).

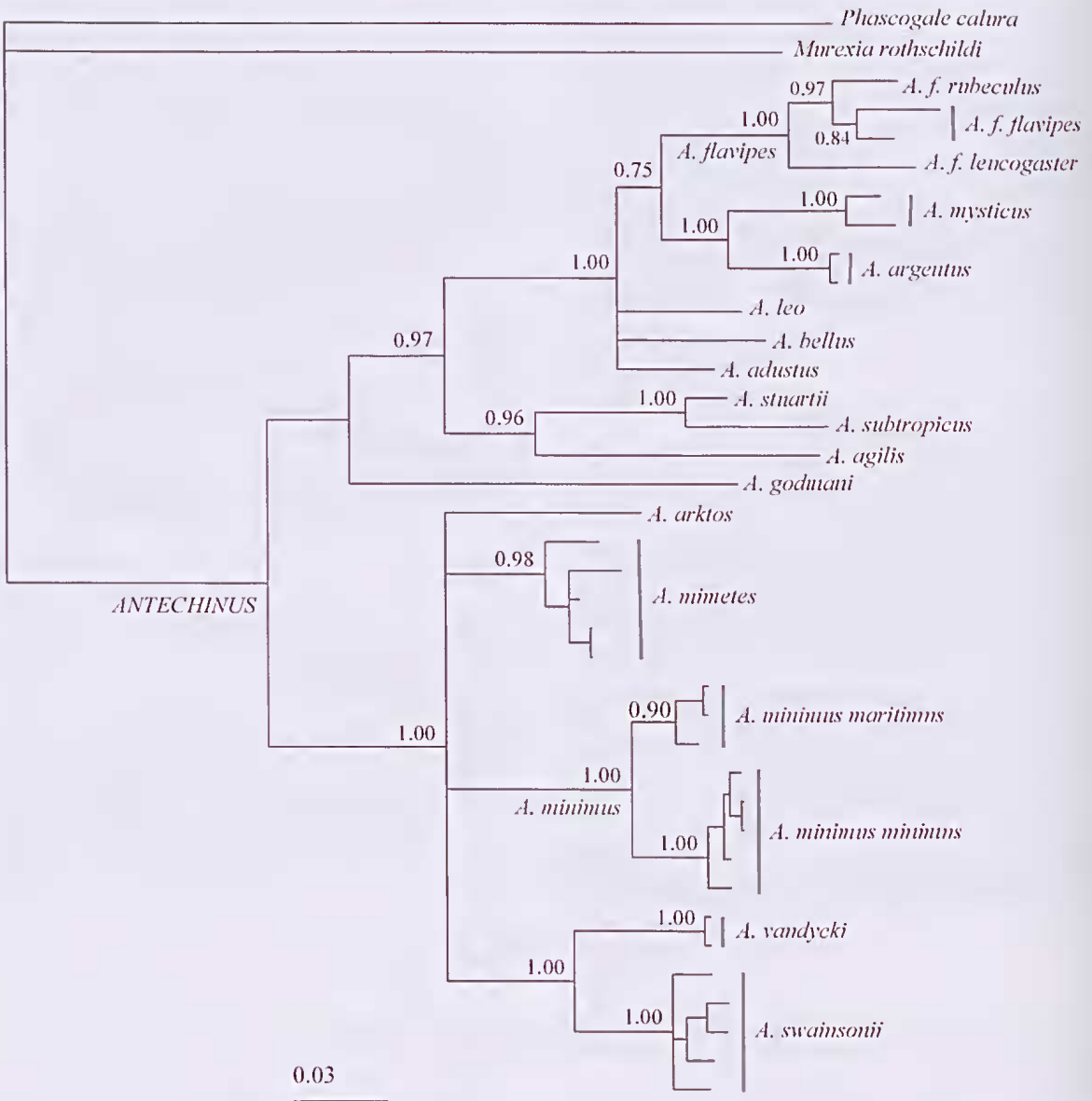


FIG. 8. Bayesian phylogeny of the genus *Antechinus* based on concatenated mitochondrial (Cytb) and nuclear (IRBP) gene sequences. Posterior probabilities are shown at each node (those less than 0.70 are omitted).

Dentition. Upper incisors. I^1 is broad, non-procumbent and relatively curved. It is taller-crowned than all other upper incisors. It is not separated from I^2 by a diastema. Left and right I^1 contact each other. For I^{2-4} , crown height: $I^4 > I^3 > I^2$. In crown length, I^{2-4} are subequal.

All upper incisors have weak buccal cingula. I^4 carries no anterior or posterior cusp. The roots of I^4 are wide.

Upper canines: C^1 is slender and almost straight, with an indistinct boundary between

root and crown. There is no buccal cingulum and no lingual cingulum. Neither an anterior cusp nor posterior cusp is present.

Upper premolars: There are no diastemata between C^1 and P^1 , P^1 and P^2 or P^2 and P^3 , although there is not quite contact between C^1 - P^1 , P^1 - P^2 or P^2 - P^3 . All upper premolars carry weak buccal and weak lingual cingula, which are more pronounced at the rear of the tooth. In crown size: $P^3 > P^2 > P^1$. Posterior cusps are present in P^3 (very large), P^2 (notably smaller than P^3) and P^1 (slightly smaller than P^2). Small anterior cusps are present in P^1 and P^2 , but not in P^3 .

Upper molars: The posterior tip of P^3 lies immediately below the prominent stylar cusp A. The anterior cingulum below stylar cusp B appears as a broad flange and is just complete. Stylar cusp B and the paracone are relatively unworn and a minute, worn protoconule is present on the trigon basin. The paracone is approximately half the height of the metacone. Stylar cusp C is just visible on L and RM^1 , but E is a worn rudiment. There is no posterior cingulum on M^1 .

In M^2 , the anterior cingulum appears as a very broad wing which contacts the metastylar corner of M^1 and tapers away quickly, as it progresses down and along the base of the paracone. It finally degenerates mesially to the base of the paracone apex. There is no protoconule. M^2 lacks stylar cusps A and C; E is a worn rudiment. Stylar cusp D is subequal in height to its condition in M^1 but is slightly more sharply peaked. The paracone is about 2.5 times the height of the metacone. There is no posterior cingulum.

In M^3 , the protocone is greatly reduced, the anterior cingulum is narrower and shorter than that in M^2 and it becomes indistinct after covering 1/2 of the distance between stylar cusp B and the base of the paracone; the anterior cingulum degenerates mesially well buccal to the base of the paracone apex. There is no evidence of an anterior cingulum at the base of the paracone, nor is there a protoconule. Stylar cusp D is reduced to a small sharp peak, barely taller than B. Stylar cusp C is low and worn, whereas E is a worn nubbin.

In M^4 , the protocone is very small and narrow, and the metastylar corner is greatly developed. The anterior cingulum is about as broad as that in M^3 , and tapers gradually away from the anterior corner of M^4 , becoming indistinct at a point just labial to the paracone apex. The paracone is large and sharply peaked. The posterior cingulum is absent. In occlusal view, the angle made between the post-protocrista and the post-paracrasta is close to 90° .

Lower incisors: In crown height: $I_1 > I_2 > I_3$. The incisors project almost horizontally from the tip of the dentary. I_1 and I_2 are oval in anterolateral view and scoop-like in occlusal view. I_3 is premolariform in lateral view with a very large posterior cusp at the base of the crest which descends posteriorly from the apex of the primary cusp; the anterior edge of C_1 rests inside this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent, heavy posterolingual lobe, and crown enamel of the primary and posterior cusps folds lingually such that the crest of the two cusps bisects the tooth longitudinally.

Lower canines: C_1 is caniniform and characterised by strong curvature from root to crown. It possesses strong buccal and lingual cingula and there is no posterior cusp.

Lower premolars: Premolars are roughly equally spaced but C_1 clearly does not contact P_1 and P_3 does not quite contact M_1 . They are well cingulated buccally and lingually and this is particularly prominent towards the rear of the tooth. In crown height: $P_2 > P_3 > P_1$. All premolars are narrow and elongate. All possess very strong posterior cusps and P_2 possesses a small anterior cusp. The bulk of each premolar mass is concentrated anterior to the line drawn transversely through the middle of the two premolar roots. Postero-lingual lobes are not a feature of the lower premolars.

Lower molars: All the molars are narrow. The M_1 talonid is wider than the trigonid and the anterior cingulum is present but very poorly developed; it terminates at the posterior base of the protoconid. There is a weak, broken buccal cingulum. The narrow paraconid appears in occlusal view as a small steeply-sided spur,

the lingual edge of which makes a considerable swelling on the endoloph of M_1 . The paracristid is almost 45° to the horizontal from paraconid to paracristid fissure and vertical from the paracristid fissure to the anterior base of the pre-protocristid. The metacristid and hypocristid are both roughly oblique to the long axis of the dentary. The cristid obliqua is long and extends from the hypoconid to the posterior wall of the trigonid, intersecting the trigonid at a point directly below the apex of the protoconid. The hypocristid terminates at the tip of the metastylid. From the metaconid posteriorly, the talonid endoloph follows the line of the dentary until the base of the hypoconulid. The entoconid is low and broadly rounded.

In M_2 , the trigonid is slightly narrower than the talonid. The anterior cingulum is poorly developed, terminating lingually in a weak parastylid notch into which the hypoconulid of M^1 is tucked, and terminating buccally at a point below the protoconid apex. There is a small, incomplete buccal cingulum at the base of the protoconid-hypoconid junction. The strong posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid. The paraconid is well developed but is the smallest trigonid cusp, smaller than the metaconid which is in turn smaller than the protoconid. The entoconid is low and broad, but about twice the height of that in M_1 . The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid, intersecting the trigonid at a point slightly buccal to the apex of the protoconid but well buccal to the metacristid fissure. The hypocristid extends from slightly anterior and buccal to the hypoconulid to the tip of the hypoconid. From the base of the metaconid posteriorly, the endoloph follows the line of the dentary axis.

In M_3 , the trigonid is as wide as the talonid. A small parastylid wraps around the hypoconulid of M_2 and there is a weak anterior cingulum on M_3 , slightly narrower than that of M_2 . Buccal and posterior cingula are as in M_2 but more poorly developed. The reduced cristid obliqua intersects the trigonid at a point just lingual to the longitudinal vertical midline drawn through the apex of the protoconid, but

slightly buccal to the metacristid fissure. The entoconid on M_3 is long and tall and crushes against the hypoconulid anterior base. The endoloph on the talonid of M_3 takes a more buccal orientation than that seen in M_2 . The rest of M_3 morphology is as in M_2 .

In M_4 , the trigonid is much wider than the talonid. The anterior cingulum is as in M_3 . The posterior cingulum is absent. Of the three main trigonid cusps, the metaconid is marginally taller than the paraconid but both are dwarfed by the almost twice as tall protoconid. The hypoconid of M_4 is absent from the talonid, as is the entoconid. The cristid obliqua forms a low, weak crest which degenerates before contacting the trigonid wall. A significant feature of M_4 morphology is the reduction of talonid crown enamel below the cristid obliqua which results in the talonid appearing (in occlusal view) as a narrow oblique spur jutting off the trigonid wall.

Skull. *Antechinus minimus minimus* is characterised by a long, narrow, low rostrum which is tubular in cross section. The rostrum rises gradually along the nasals, then more steeply through the frontals to a high, domed cranium. The nasals are narrow anteriorly and flare very wide posteriorly. In lateral view, there is minimal depression of the rostrum at the junction of the frontals and nasals, and the posterior dorsal surface of the skull is only gently curved across the cranium. The right and left alisphenoid bullae are moderately enlarged and widely separated. The basicranium is smashed behind the alisphenoid bullae. The right foramen pseudovale appears to have been reasonably small and kidney-shaped. The large premaxillary vacuities extend from the level of the I^2 root back to the level of the anterior root of P^1 . The large maxillary vacuities extend from the level of the anterior of the protocone root of M^1 back as far as the level of the posterior of the protocone root of M^3 .

Material Examined. Bridport $41^\circ 00' S 147^\circ 23' E$ (QVM 1987.1.29, QVM 1987.1.82, QVM 1986.1.3, QVM 1986.1.47, QVM 1988.1.84); Brooks Creek (QVM 1981.1.113, QVM 1981.1.102, QVM 1981.1.53, QVM 1981.1.47, QVM 1981.1.68, QVM 1981.1.45, QVM 1981.1.44, QVM 1981.1.101, QVM 1981.1.106, QVM

Swamp Antechinus, *Antechinus minimus* (È. Geoffroy)

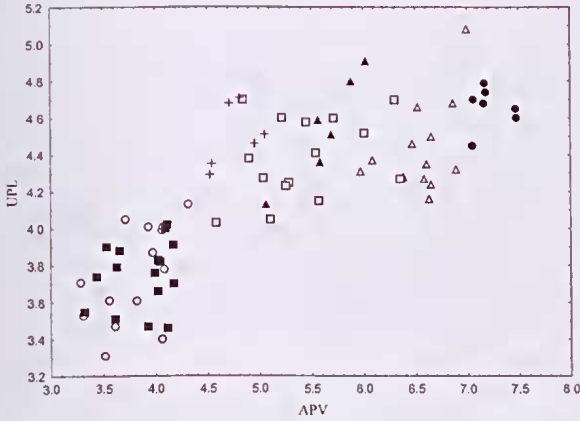


FIG. 9. Scatterplot of anterior palatal vacuity length (APV) versus upper premolar row length (UPL) measures for male *A. minimus minimus* (○), *A. minimus maritimus* (■), *A. swainsonii* (△), *A. vandycki* (●), *A. mimetes mimetes* (□), *A. mimetes insulanus* (▲) and *A. arktos* (+).

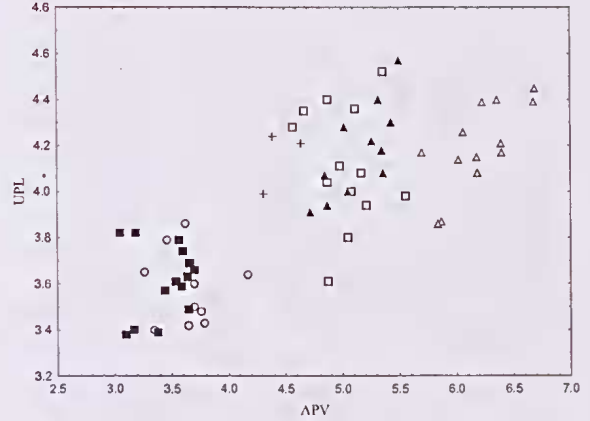


FIG. 10. Scatterplot of anterior palatal vacuity length (APV) versus crown length of upper premolar row (UPL) measures for female *A. minimus minimus* (○), *A. minimus maritimus* (■), *A. swainsonii* (△), *A. vandycki* (●), *A. mimetes mimetes* (□), *A. mimetes insulanus* (▲) and *A. arktos* (+).

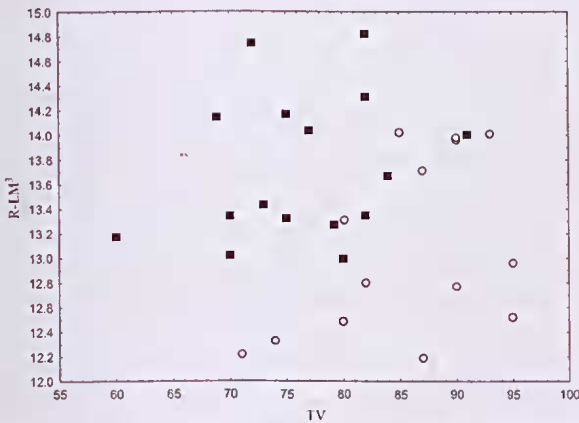


FIG. 11. Scatterplot of tail-vent length (tv) versus skull width level with the junction of the third and fourth upper molars (R-LM³) measures for male *A. minimus minimus* (○), *A. minimus maritimus* (■), *A. swainsonii* (△), *A. vandycki* (●), *A. mimetes mimetes* (□), *A. mimetes insulanus* (▲) and *A. arktos* (+).

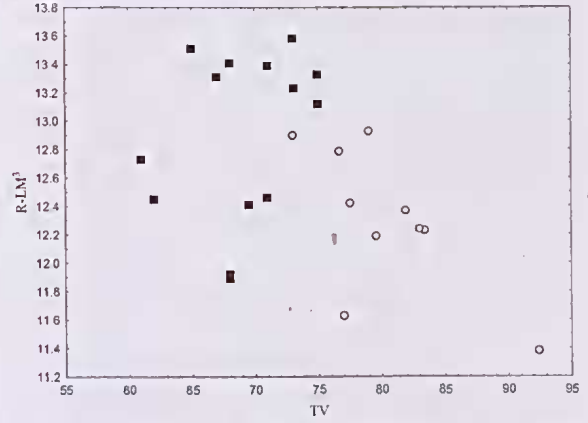


FIG. 12. Scatterplot of tail-vent length (tv) versus skull width level with the junction of the third and fourth upper molars (R-LM³) measures for female *A. minimus minimus* (○), *A. minimus maritimus* (■), *A. swainsonii* (△), *A. vandycki* (●), *A. mimetes mimetes* (□), *A. mimetes insulanus* (▲) and *A. arktos* (+).

1981.1.48, QVM 1981.1.105, QVM 1981.1.85); Bruny Island, Tasmania 43°21' S 147°19' E (MTAS A1500); Cockle Creek, Tasmania 43°36' S 146°51' E (QM JM20118); Eriba - Cradle Mt. Rd 41°39' S 145°57' E (QVM 1963.1.70); Flinders Is, Tasmania 40°01' S 148°02' E (MVIC C21965); Fortescue Bay, Tasmania 43°09' S 147°57' E (QM JM20118); Hummock Island, Bass Strait 40°26' S 144°54' E (BMNH 58.12.27.120);

Lake Pedder, Tasmania 42°57' S 146°12' E (MTAS A801, MTAS A802); Maatsuyker Island 43°39' S 146°17' E (MTAS A610, MTAS A611, MTAS A612, MTAS A616, MTAS A617, MTAS A618, MTAS A872; MVIC C216, MVIC C217, MVIC C6337, MVIC C6338, MVIC C6339); Martha Lavinia Beach, King Is 39°39' S 144°04' E (QVM 1986.1.52); Mount Direction, Tasmania 41°15' S 147°01' E (QVM 1988.1.45); Queenstown, Tasmania 42°05' S

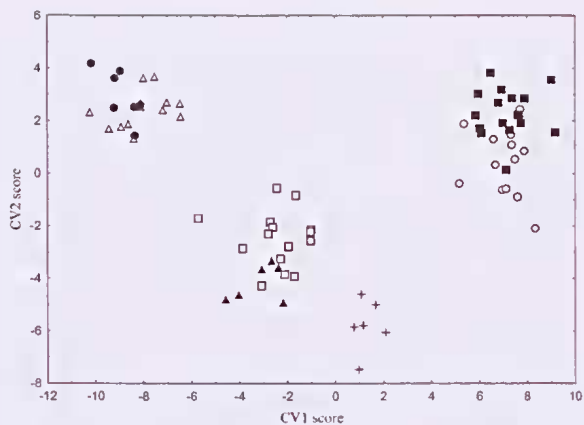


FIG. 13. Scatterplot of canonical variates scores (roots 1 and 2) for male *A. minimus minimus* (○), *A. minimus maritimus* (■), *A. swainsonii* (Δ), *A. vandycki* (●), *A. mimetes mimetes* (□), *A. mimetes insulanus* (▲) and *A. arktos* (+).

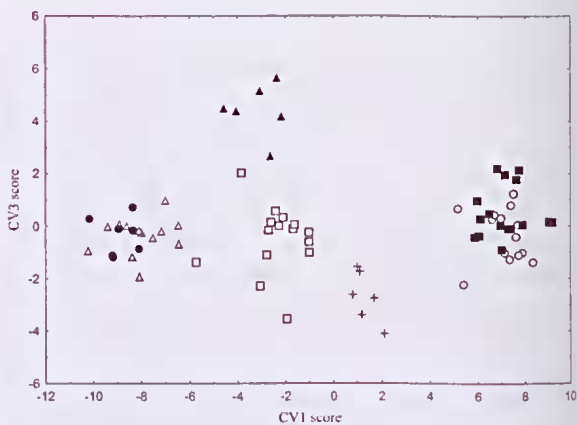


FIG. 14. Scatterplot of canonical variates scores (roots 1 and 3) for male *A. minimus minimus* (○), *A. minimus maritimus* (■), *A. swainsonii* (Δ), *A. vandycki* (●), *A. mimetes mimetes* (□), *A. mimetes insulanus* (▲) and *A. arktos* (+).

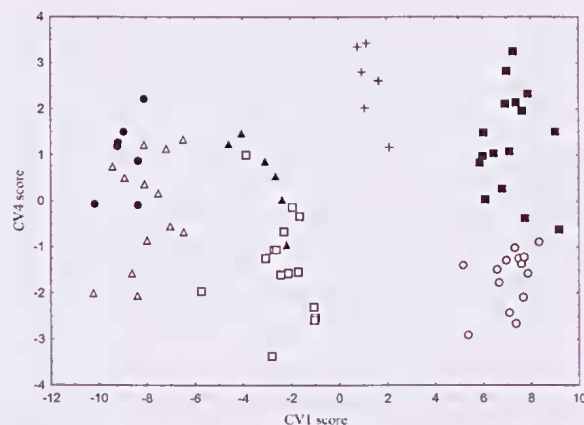


FIG. 15. Scatterplot of canonical variates scores (roots 1 and 4) for male *A. minimus minimus* (○), *A. minimus maritimus* (■), *A. swainsonii* (Δ), *A. vandycki* (●), *A. mimetes mimetes* (□), *A. mimetes insulanus* (▲) and *A. arktos* (+).

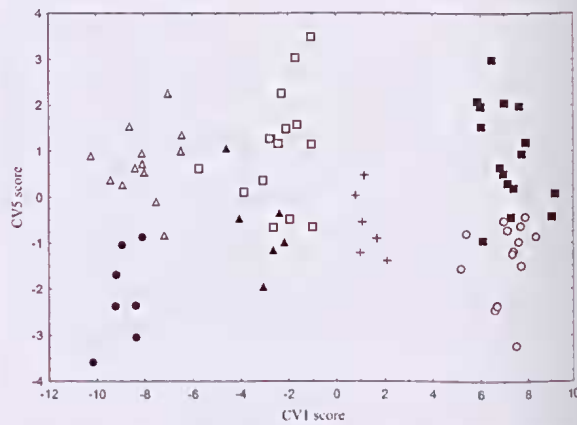


FIG. 16. Scatterplot of canonical variates scores (roots 1 and 5) for male *A. minimus minimus* (○), *A. minimus maritimus* (■), *A. swainsonii* (Δ), *A. vandycki* (●), *A. mimetes mimetes* (□), *A. mimetes insulanus* (▲) and *A. arktos* (+).

145°33'E (QVM 2014.1.15, QVM 1998.1.1); South Mount Cameron, Tasmania 41°02' S 147°57'E (QVM 1944.1.57); Tasmania (BMNH 52.1.15.7); Turners Marsh 41°16' S 147°08'E (QVM 2007.1.2); Waratah 41°27' S 145°32'E (QVM 1963.1.213, QVM 1963.1.214, QVM 1963.1.134, QVM 1963.1.212, QVM 1963.1.161, QVM 1963.1.162, QVM 1963.1.125, QVM 1963.2.123, QVM 1963.1.163).

Autechinus minimus maritimus
(Finlayson, 1958)

Phascogale swainsonii maritima, Finlayson 1958

Material examined. Holotype. South Australian Museum, SAM M4985. Adult male in spirit with the skull extracted; both spirit and skull components are in good condition (refer Fig 4). Collected by G.H.Tilley.

Swamp Antechinus, *Antechinus minimus* (È. Geoffroy)

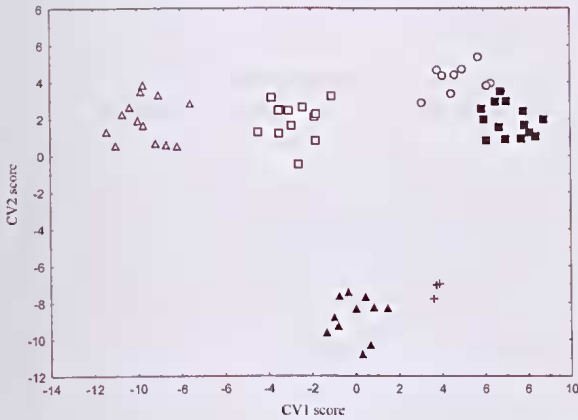


FIG. 17. Scatterplot of canonical variates scores (roots 1 and 2) for female *A. minimus minimus* (○), *A. minimus maritimus* (■), *A. swainsonii* (△), *A. vandycki* (●), *A. mimetes mimetes* (□), *A. mimetes insulanus* (▲) and *A. arktos* (+).

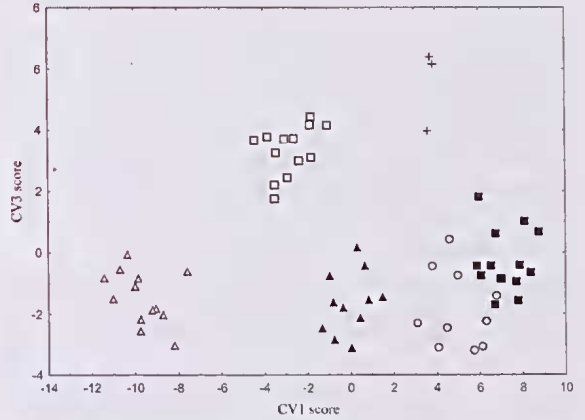


FIG. 18. Scatterplot of canonical variates scores (roots 1 and 3) for female *A. minimus minimus* (○), *A. minimus maritimus* (■), *A. swainsonii* (△), *A. vandycki* (●), *A. mimetes mimetes* (□), *A. mimetes insulanus* (▲) and *A. arktos* (+).

Type locality. Port MacDonnell, south-eastern South Australia, 38°03'S 140°42'E at sea level.

Rediagnosis. There are no statistically significant morphological differences between *A. minimus maritimus* and *A. minimus minimus*. However, *A. minimus maritimus* differs from *A. minimus minimus* in having a typically broader skull at a point level with the molar teeth and often larger upper and lower second molar teeth. *Antechinus minimus maritimus* also tends to have a shorter tail and smaller feet than *A. minimus minimus*. *Antechinus minimus maritimus* differs from all members of the Dusky Antechinus complex in having a leaden grey head merging to yellowish (rather than brownish) rump. Also, *A. minimus maritimus* tends to have a heavier rump and markedly shorter tail (especially) relative to body length compared to all members of the Dusky Antechinus complex. *Antechinus minimus maritimus* is easily distinguished from all other antechinus species, being typically larger, heavier bodied, relatively shorter tailed (compared to head-body length) and smaller-eared; also, the snout is relatively longer / narrower with relatively long anterior palatal vacuities compared to most other antechinus species outside the Dusky Antechinus complex.

Description of Holotype. Pelage. We have not examined the alcoholic body of this holotype, but a detailed description is provided by Finlayson (1958) who described it thus, 'the head, nape and shoulders a cold, grizzled grey increasingly suffused posteriorly with rufous which may become very rich over the rump... Ventrums a uniform greyish white, but variably and sometimes strongly washed with yellow or buff and deep plumbeous for the basal two thirds.' (p. 149)

Dentition. I¹ contacts I². In crown height: I²>I³>I⁴. I⁴ carries no anterior or posterior cusp. C¹ has no posterior cusp. In the upper premolars, slight diastemata occur between C¹-P¹, P¹-P² and P²-P³. The gap separating P¹ and P² is greater than that separating P² and P³ and greater than that separating C¹ and P¹. In M⁴, the angle made between post-protocrista and post-paracrista is close to 135°. Lower premolars with P₁ just contacting P₂ and P₃ is in contact with M₁. The rest of the craniodental features are as for the holotype of *A. minimus minimus* described above.

Skull. The left and right alisphenoid tympanic bullae are very widely separated. The foramen pseudovale is large, as is the eustachian canal opening. The internal jugular canal foramina are moderately large and the canals are only poorly raised and non-prominent. The posterior lacerate foramina are small, while the

entocarotid foramina are large. The maxillary vacuities extend from the level of the M¹ protocone root back as far as the level of the M³ metacone root. The larger left premaxillary vacuity extends from the level of the I² root back to the level of the posterior edge of C¹; the smaller right premaxillary vacuity terminates at the level of the middle of the C₁ root.

Material examined. Anglesea 38°25'S 144°11'E (MVIC C26888, C27051, C27042, C27044, C27045, C27039, C27050, C27062, C27064, C27065, C27048, C26986, C29803); Birnam Otways, Victoria 38°27'S 143°35'E (MVIC C26485); Bridgewater Lakes 38°19'S 141°24'E (MVIC C13820, MVIC C13863, MVIC C15878); Buck's Lake, South Australia 37°55'S 140°24'E (SAM M11464); Cape Liptrap, Victoria 38°54'S 145°56'E (MVIC C31198); Carpenter Rocks, South Australia 37°54'S 140°23'E (SAM M11978, SAM M12996); Casterton 37°36'S 141°24'E (MVIC C27030, C27043, C27031, C27041); Dartmoor 37°55'S 141°16'E (MVIC C24345, MVIC C24347, MVIC C26889, MVIC C27047, MVIC C27049); Greater Glennie Island 39°05'S 146°15'E (MVIC C13830, C13829, C13822); Hut Gully, Victoria (MVIC C13818, C13819, C22156); Kennett River Foreshore, Otways, Victoria 38°40'S 143°51'E (MVIC C11619); Kilcun, 2 km west (MV C13447); Kongorong 37°54'S 140°33'E (SAM M10052); Millicent, South Australia 37°35'S 140°21'E (SAM M22405); Moonlight Head 38°46'S 143°14'E (MVIC C13826); Mount Roundback, Victoria 38°52'S 146°26'E (MVIC C17100); Otways, Victoria 38°27'S 143°58'E (MVIC C11619); Parker River Inlet 38°50'S 143°33'E (SAM M4985); near Point Danger, Portland, Victoria 38°21'S 144°20'E (MVIC C23475); Port Campbell NP, Victoria 38°37'S 143°00'E (MVIC C22199); Port MacDonnell 38°03'S 140°42'E (SAM M4985); Snake Island, Victoria 38°45'S 146°34'E (MVIC C26018); Southend, South Australia 37°34'S 140°08'E (SAM M10930); Tucker Orchard, Victoria 38°34'S 143°29'E (MVIC C26831); Upper Yarra, Victoria 37°42'S 145°50'E (MVIC C6351); Venus Bay, Victoria 38°40'S 145°47'E (MVIC C36842); Yanakie 38°49'S 146°13'E (MVIC C25817).

SYNONYMS

The status of *Phascogale affinis* Gray, 1841

Syntypes. BMNH 41.1241, puppet skin and skull (skin in good condition, skull broken and basicranium missing) (refer Figs 5-6). Collected by J. Gould.

Type Locality. Tasman Peninsula, Tasmania. Altitude not supplied.

Description. Holotype BMNH 41.1241 differs from *Antechinus minimus minimus* in the following respects:

Pelage. The fur of the mid-back is 13 mm long with the basal 10 mm Slate Colour, median 2 mm Buckthorn Brown and the apical 1 mm black. The back appears overall to be a speckled Olive Brown. Medially-thickened guard hairs are interspersed thickly through the fur and are 15 mm long on the rump and reduce to 6 mm where they terminate at the crown of the head. Fur on and below the shoulders, thighs flanks and chin lacks the black tips or coarse guard hairs and these areas and the belly appear as Old Gold. There is no head stripe and no eye-ring. The soft ventral fur (10 mm long on the belly) is Mouse Gray on the basal 2/3 and Naples Yellow on the apical 1/3 and is interspersed by Naples Yellow medially-thickened spines 13 mm long. The belly is thus an overall Old Gold. Forefeet and thinly covered with Olive Brown hairs. Hindfeet are more thickly covered with lighter Buffy Brown coloured hairs. The tail is weakly bicoloured with hairs averaging 3 mm along its length and increasing 4 mm at its tip. Dorsally the hairs are a uniform Olive Brown with Fuscous Black tips. Ventrally, the black tips are lost and the overall colour is Buffy Brown.

Vibrissae. Approximately 16 mystacial vibrissae occur on each side of the face; they are, however, twisted and broken off, and are a maximum length of 11 mm. Supra-orbital vibrissae could not be located; genals (Fuscous Black and Colourless) number 3 (left) and 4 (right); ulna-carpals (colourless) number 3 on the right (left vibrissae could not be found). No submentals could be found.

Tail. The tail is slightly shorter than the nose-vent length. It is thin and tapers toward the tip.

Hindfoot. The claws are long. The apical granule of the hindfoot is elongated, enlarged and striate. The enlarged hallucal pad is just separate from the post-hallucal pad. Metatarsal granules are not visible in the holotype.

Ears. The ears are small and the supratragus appears to be simple and flat.

Dentition. I¹ is separated from I² by a slight diastema. In crown height: I²>I³>I⁴. I⁴ carries no anterior or posterior cusp. C¹ has a large posterior cusp. In the upper premolars, diastemata occur between C¹-P¹, P¹-P², P²-P³. The gap separating P¹ and P² is greater than that separating P² and P³ is greater than that separating C¹ and P¹. In the upper molars, stylar cusp B is very large in M¹ which also lacks a posterior cingulum. In M², stylar cusp B is again very large. Stylar cusp C is present and D is reduced in comparison to M¹ but is still very large. In M³, the anterior cingulum is as large as it is in M² and it becomes indistinct after covering 1/2 the distance between stylar cups B and the base of the paracone. In M⁴, the angle made between post-protocrista and post-paracrista is close to 90°. Lower premolars are equally spaced with P₃ in contact with M₁. In M₃, the entoconid is seen to crush against the hypoconulid and in M₄ a small entoconid is present. A tall hypoconid is also present and the cristid obliqua intersects the trigonid wall well lingual to the metacrista fissure. There is no hypoconulid.

Skull. The entire basicranium is smashed and missing posterior from the maxillary vacuities. The premaxillary vacuities extend from the level of the I² root back to the level of the middle of P¹. The larger maxillary vacuities extend from the level of the protocone root of M¹, but are open-ended posteriorly with the missing basicranium.

Note. When Gray (1841) described *Phascogale affinis* (the description is a catalogue listing), he and Gould (from whom he obtained the specimen) and, perhaps more reluctantly, Waterhouse (at least by 1841), considered *A. minimus* and *A. swainsonii* synonymous (see Gray, 1841: 401). Of his *P. affinis*, Gray (1841) maintained 'This may be the same *P. minima* of Geoffroy, but the tail is longer for its size' (p. 407). Gray lists two specimens collected (nominations of holotypes was not practised at that stage), a male and a female; however, BMNH 1841.1241 is the only specimen of the pair now represented

in the research collection of the British Museum (Natural History) ('one of two syntypes, location of other specimen unknown', Jenkins & Knutson, 1983). The sex of the remaining specimen is not identified on attached labels, nor is it immediately apparent from the skin. Our interest in the sex of the holotype centres on a possibility that the missing syntype may have been an example of *A. swainsonii* or *A. vaudycki* and not *A. minimus*. Measurements provided by Gray for the female (HB: 4.5" [114 mm]; T: 2.75" [70 mm]) sit comfortably within the range of measurements from females available today (taking into account that for head-body/tail lengths, the 'root' of the tail was where head-body and tail measurements ended, not the 'vent'); for total length in female *A. minimus* \bar{x} = 178.83, R = 165 - 203, N = 12 (data from Green, 1972), \bar{x} = 175.4, R = 165 - 182, N = 5 (our research), for total length in males \bar{x} = 195.5, R = 174 - 230, N = 10 (data from Green, 1972), \bar{x} = 190.2, R = 174 - 204 (N = 5, our research). However, data provided for the male type specimen (HB: 6.5" [165 mm]; T: 4.5" [114 mm]) describes an extraordinarily large animal (total length 279 mm), well outside the maximum values available from our research (226 mm, MV C13826 from Moonlight Head Victoria), or from Green (1972), whose maximum value (230 mm) exceeded that provided by Wakefield and Warneke (1963). Indeed, so large is the animal described by Gray (1841), that it falls just outside those values available for the maximum total length of males of the much larger *A. swainsonii* (253 mm, N = 8, Green [1972]). The short tail length, for which *P. affinis* was named (4.5" [114 mm]) is 43 mm longer than the longest 'Tasmanian' record available to us for a male specimen of *A. minimus* (MTAS A1404, adult male, TV = 71 mm, Cockle Creek) and 14 mm longer than the longest record available to Wakefield and Warneke (1963) (TV = 100 mm, registration and provenance details unavailable). The length, however, is compatible with the upper limit of values available for males of *A. swainsonii*. Having obtained the specimens from Gould, it is not unreasonable to suggest the published values could have represented field measurements, particularly as neither of Gray's published

measurements (total length for male = 11" [279 mm]; female = 7.25" [184 mm]) correspond with the total length of the study skin BMNH 41.1241 = 237 mm).

Sexual dimorphism for body size (reflected through cranial and dental morphology) is at its most insignificant in this species (compared with e.g., *A. godmani*). The sex of BMNH 1841.1241, therefore, could not be established on these grounds. If the puppet skin of BMNH 1841.1241, which shows no evidence of a scrotum, is in fact the female referred to by Gray (1841), then the preparation of the skin has resulted in the addition of 33 mm to the overall length. If, on the other hand, BMNH 1841.1241 is the male, with scrotum removed, preparation must account for shrinkage of approximately 53 mm.

Gray noted that the male was darker. This could further implicate an example of *A. swainsonii* as Green (1972) found no sexual dimorphism for pelage colour in *A. minimus*; however, ranges in depth of pelage colour from 1 to 3 (where 5 represents almost black pelage, 1 represents light fawn-brown) have been recorded (Van Dyck, S. pers. obs.) from individuals collected at a particular locality (e.g., Brooks Ck) in Tasmania.

Given that *A. affinis* was described for the relatively short length of its tail, and taking into account the other factors mentioned above, we suggest that one of Gray's syntypes was an example of *A. minimus* and the other, an example of *A. swainsonii*; the surviving syntype, BMNH 1841.1241, is most likely the (slightly stretched) *A. minimus* female.

Antechinus concinnus Higgins and Petterd
(1883) *incertae sedis*

The sex and locality of this specimen in Tasmania is unknown; no registration number; formerly in the collection of the Royal Society of Tasmania; holotype lost. This novelty has, in the past, been assigned to the synonymy of *A. minimus* (Thomas, 1888; Iredale & Troughton, 1934; Tate, 1947; Wakefield & Warneke, 1963; Mahoney & Ride, 1988, who corrected the publication date from 1884 to 1883) probably

on the authority of Thomas (1888) who may not have even examined the specimen. The animal is small (total length = 203.6 mm) and could pass for a young *A. swainsonii* or an adult *A. minimus*. Green (1972) used the change in dorsum pelage colour from dark brownish grey to rich tan over the rump, flanks and round the base of the tail to distinguish adult *A. minimus* from *A. swainsonii*. If the holotype was an adult *A. minimus*, however, Higgins and Petterd make no mention of a warming change in dorsal pelage colour, although they describe the fur as 'brownish-grey on the upper surface'. Considering all the above, we consider this form to be *incertae sedis*.

SPECIES BY SPECIES COMPARISONS

All tests for normality and variance homogeneity of samples used in morphometric analyses were non-significant at $p=0.05$.

Phylogenetic Structure

Figures 7-8 suggest that there are 15 putative species within antechinus. The phylogenies show the four species comprising the Dusky Antechinus complex and *A. minimus* clade is well-supported and deeply divergent compared with all congeners. Each of the four species of Dusky Antechinus and *A. minimus* are strongly supported and monophyletic with respect to each other; however, species-level sister relationships between these taxa are unclear with the exception of the well-supported sister Dusky Antechinus from Tasmania, *A. swainsonii* and *A. vandycki* (Figs 7-8). Within *A. minimus*, *A. minimus minimus* (Tasmania) and *A. minimus maritimus* (mainland) are strongly-supported (0.9-1.0 posterior probabilities) and reciprocally monophyletic; there is moderate genetic divergence within each subspecies.

Figure 7 is a phylogeny generated from mitochondrial (Cytochrome B - CytB) data and Fig. 8 combines the data from one mitochondrial gene (Cytochrome B - CytB) and one nuclear gene (Interphotoreceptor Binding Protein - IRBP); both phylogenies accord in their structuring of putative species clades which, once matched with morphological vouchers, then form the

Swamp Antechinus, *Antechinus minimus* (È. Geoffroy)

TABLE 1. Univariate statistics: means, standard deviations and range minima and maxima of measured variables for *Antechinus minimus minimus*.

	MALES					FEMALES					
	Valid N	Mean	Min	Max	St. Dev.		Valid N	Mean	Min	Max	St. Dev.
wt	13	74.38	37.00	118.00	30.05	wt	7	38.43	24.00	58.00	11.93
hb	13	130.68	114.00	155.00	14.66	hb	13	112.64	103.00	132.00	8.56
tv	13	85.31	71.00	95.00	7.61	tv	13	78.19	68.00	92.40	6.33
hf	14	19.98	18.00	22.50	1.33	hf	12	18.41	17.00	20.56	1.28
e	14	14.94	13.00	19.00	1.61	e	13	14.05	12.78	15.00	0.59
APV	14	3.81	3.28	4.31	0.31	APV	10	3.65	3.26	4.17	0.26
BL	14	28.71	26.32	31.46	1.56	BL	10	26.27	24.93	27.60	0.94
Dent	14	23.16	21.54	25.04	1.12	Dent	10	21.07	19.92	22.34	0.76
IBW	14	4.63	4.13	5.08	0.29	IBW	10	4.37	4.02	4.82	0.25
IOW	14	7.78	7.36	8.27	0.27	IOW	10	7.45	7.11	7.76	0.21
IPV	14	4.05	3.37	4.59	0.39	IPV	10	3.42	3.08	3.90	0.27
M ² W	14	2.27	2.13	2.40	0.07	M ² W	10	2.16	2.08	2.20	0.04
NW	14	2.75	2.39	3.18	0.23	NW	10	2.70	2.33	2.93	0.16
OBW	14	12.32	11.42	12.91	0.44	OBW	10	11.52	11.14	12.22	0.31
PPV	14	5.04	4.00	6.05	0.54	PPV	10	4.77	4.45	5.14	0.28
R-LC ¹	14	5.18	4.80	5.60	0.26	R-LC ¹	10	4.67	4.30	5.14	0.26
R-LM ¹	14	9.10	8.51	9.66	0.42	R-LM ¹	10	8.65	8.12	9.07	0.30
R-LM ¹ T	14	7.82	7.45	8.52	0.37	R-LM ¹ T	10	7.37	7.01	7.68	0.22
R-LM ²	14	10.85	10.02	11.90	0.69	R-LM ²	10	10.33	9.49	10.83	0.46
R-LM ³	14	13.09	12.19	14.02	0.72	R-LM ³	10	12.31	11.38	12.93	0.51
ZW	14	16.95	15.66	18.74	1.01	ZW	10	15.32	14.44	15.94	0.57
HT	14	10.66	9.87	11.34	0.49	HT	10	10.13	9.83	10.55	0.21
PL	14	16.52	15.63	17.77	0.66	PL	10	15.20	14.61	16.00	0.49
SWR-LC ¹ B	14	4.54	4.20	4.85	0.22	SWR-LC ¹ B	10	4.07	3.80	4.48	0.20
TC	14	2.92	2.67	3.21	0.18	TC	10	2.69	2.52	2.89	0.12
NWR	14	4.66	4.13	5.32	0.35	NWR	10	4.32	3.89	4.80	0.35
PML	14	8.79	7.72	9.53	0.55	PML	10	7.92	7.66	8.52	0.26
UML	14	6.48	6.11	6.89	0.26	UML	10	6.21	5.95	6.51	0.20
HT-B	14	8.52	8.01	9.11	0.38	HT-B	10	8.06	7.59	8.59	0.31
BuL	14	4.17	3.86	4.37	0.14	BuL	10	3.84	3.49	4.03	0.16
I ¹ -P ³	14	9.03	8.34	9.72	0.43	I ¹ -P ³	10	8.30	7.99	8.65	0.23
LML	14	6.96	6.60	7.41	0.24	LML	10	6.73	6.48	7.08	0.21
I ₁ -P ₃	14	7.26	6.83	7.65	0.29	I ₁ -P ₃	10	6.56	6.17	7.10	0.27
M ₂ W	14	2.06	1.98	2.16	0.06	M ₂ W	10	2.02	1.90	2.10	0.06
UPL	14	3.75	3.31	4.13	0.27	UPL	10	3.58	3.40	3.86	0.16

basis for testing individual assignment based on craniodental variation in subsequent multivariate analyses. Although the majority of the phylogenetic signal is generated from the mtDNA data, the nuclear gene corroborates the interspecific mitochondrial clade structure.

Bivariate Scatterplots

A range of scatterplots are shown for dental variables differentiating *A. minimus* from the four species (five taxa) of Dusky Antechinus. Figs 9-10 show differences among these taxa for

TABLE 2. Univariate statistics: means, standard deviations and range minima and maxima of measured variables for *Antechinus minimus maritimus*.

MALES						FEMALES					
	Valid N	Mean	Min	Max	St. Dev.		Valid N	Mean	Min	Max	St. Dev.
wt	6	62.27	42.00	91.00	18.33	wt	5	44.20	35.00	60.00	9.68
hb	11	123.49	99.98	148.00	15.18	hb	8	108.94	91.00	123.00	10.53
tv	11	77.09	60.00	97.93	9.87	tv	8	70.20	62.00	75.00	4.35
hf	11	18.57	17.20	20.00	0.79	hf	7	17.33	16.00	18.20	0.78
e	10	15.03	13.10	17.00	1.15	e	6	14.80	14.01	16.00	0.80
APV	16	3.87	3.32	4.17	0.28	APV	14	3.45	3.05	3.70	0.23
BL	16	28.77	27.14	32.25	1.42	BL	14	26.82	24.52	28.11	0.94
Dent	16	23.19	21.80	26.00	1.09	Dent	14	21.47	19.97	22.34	0.63
IBW	16	4.49	3.99	5.09	0.30	IBW	14	4.31	3.84	4.62	0.23
IOW	16	7.47	7.07	7.98	0.25	IOW	14	7.34	6.88	7.71	0.25
IPV	16	3.91	3.52	4.64	0.32	IPV	14	3.77	3.28	4.52	0.38
M ₂ W	16	2.29	2.16	2.50	0.08	M ₂ W	14	2.27	2.16	2.45	0.09
NW	16	2.73	2.32	3.25	0.24	NW	14	2.61	2.36	2.85	0.16
OBW	16	12.31	11.82	13.76	0.52	OBW	14	11.70	11.22	12.04	0.29
PPV	16	5.13	4.04	6.02	0.50	PPV	14	4.92	4.46	5.25	0.21
R-LC ¹	16	5.27	4.86	5.81	0.31	R-LC ¹	14	4.77	4.43	5.00	0.19
R-LM ¹	16	9.42	8.94	10.11	0.35	R-LM ¹	14	8.80	8.45	9.09	0.22
R-LM ¹ T	16	8.05	7.59	8.49	0.26	R-LM ¹ T	14	7.65	6.97	8.08	0.29
R-LM ²	16	11.45	10.65	12.59	0.59	R-LM ²	14	10.82	9.94	11.44	0.47
R-LM ³	16	13.74	12.99	14.82	0.59	R-LM ³	14	12.91	11.89	13.58	0.59
ZW	16	17.00	15.73	19.23	1.08	ZW	14	15.72	14.40	16.73	0.61
HT	16	10.61	9.71	11.70	0.53	HT	14	10.20	9.60	10.78	0.30
PL	16	16.43	15.48	18.26	0.76	PL	14	15.47	14.51	16.20	0.55
SWR-LC ¹ B	16	4.69	4.16	5.13	0.27	SWR-LC ¹ B	14	4.23	3.84	4.49	0.20
TC	16	2.75	2.48	3.10	0.15	TC	14	2.63	2.45	2.83	0.13
NWR	16	4.58	3.59	5.34	0.48	NWR	14	4.34	3.88	4.84	0.32
PML	16	9.20	8.63	10.01	0.38	PML	14	8.36	7.85	8.85	0.32
UML	16	6.50	6.34	6.72	0.12	UML	14	6.38	6.18	6.67	0.16
HT-B	16	8.42	7.69	9.23	0.43	HT-B	14	8.10	7.63	8.47	0.23
BuL	16	4.17	3.73	4.66	0.21	BuL	14	4.04	3.79	4.29	0.17
I ¹ -P ³	16	9.02	8.29	9.87	0.38	I ¹ -P ³	14	8.50	7.82	8.89	0.28
LML	16	7.08	6.67	7.35	0.19	LML	14	7.02	6.74	7.33	0.21
I ₁ -P ₃	16	7.17	6.60	7.90	0.30	I ₁ -P ₃	14	6.76	6.15	7.16	0.29
M ₂ W	16	2.10	2.00	2.19	0.07	M ₂ W	14	2.08	2.00	2.19	0.06
UPL	16	3.75	3.46	4.02	0.18	UPL	14	3.61	3.38	3.82	0.15

the most discriminating dental characters: APV and UPL, for males and females, respectively. There is no overlap in APV between *A. minimus* and the four species in the Dusky Antechinus complex, with *A. minimus* having smaller anterior

palatal vacuities; within the Dusky Antechinus complex, larger vacuities tend to be a feature of higher latitude species, with smaller holes and larger gaps as one moves into lower latitudes. *Antechinus vandycki* from Tasman Peninsula, for

Swamp Antechinus, *Antechinus minimus* (É. Geoffroy)

TABLE 3. Univariate statistics: means, standard deviations and range minima and maxima of measured variables for *Antechinus swainsonii*.

MALES						FEMALES					
	Valid N	Mean	Min	Max	St. Dev.		Valid N	Mean	Min	Max	St. Dev.
wt	11	63.16	42.30	93.00	14.53	wt	15	41.59	31.00	57.00	7.36
hb	12	133.61	111.30	161.00	13.06	hb	16	116.70	103.19	127.00	8.69
tv	12	97.90	89.00	110.00	6.53	tv	16	87.75	77.00	101.42	6.13
hf	12	21.84	20.00	24.00	1.27	hf	15	19.30	18.00	21.00	0.81
e	12	16.86	15.01	21.00	1.47	e	14	15.28	14.50	16.00	0.54
APV	13	6.56	5.97	7.00	0.29	APV	13	6.20	5.70	6.69	0.30
BL	13	30.29	28.54	32.39	1.27	BL	13	28.70	26.80	30.36	1.17
Dent	13	24.62	23.05	26.61	1.19	Dent	13	23.28	21.74	24.72	0.94
IBW	13	4.50	4.15	4.81	0.19	IBW	13	4.33	4.14	4.65	0.15
IOW	13	7.95	7.61	8.77	0.30	IOW	13	7.84	7.38	8.43	0.34
IPV	13	2.14	1.77	2.74	0.31	IPV	13	2.01	1.66	2.95	0.32
M ² W	13	2.29	2.19	2.38	0.06	M ² W	13	2.22	2.08	2.34	0.08
NW	13	2.45	2.03	2.85	0.20	NW	13	2.45	2.20	2.73	0.16
OBW	13	12.24	11.31	13.30	0.54	OBW	13	11.80	11.21	12.18	0.29
PPV	13	5.33	4.39	5.99	0.44	PPV	13	5.00	4.52	5.56	0.30
R-LC ¹	13	4.64	3.99	5.20	0.33	R-LC ¹	13	4.27	3.93	4.56	0.20
R-LM ¹	13	8.52	7.70	9.07	0.47	R-LM ¹	13	8.32	7.78	8.67	0.31
R-LM ¹ T	13	7.64	7.08	8.10	0.36	R-LM ¹ T	13	7.35	6.99	7.72	0.25
R-LM ²	13	10.42	9.58	11.27	0.51	R-LM ²	13	10.01	9.48	10.51	0.30
R-LM ³	13	12.73	11.89	13.64	0.53	R-LM ³	13	12.17	11.21	12.59	0.40
ZW	13	16.68	15.43	18.49	0.97	ZW	13	15.63	14.16	16.42	0.58
HT	13	10.50	9.79	10.99	0.40	HT	13	10.10	9.61	10.77	0.37
PL	13	17.85	16.97	19.19	0.68	PL	13	17.08	15.91	17.87	0.62
SWR-LC ¹ B	13	4.18	3.74	4.75	0.29	SWR-LC ¹ B	13	3.81	3.54	4.16	0.21
TC	13	2.52	2.21	2.91	0.19	TC	13	2.62	2.22	2.87	0.21
NWR	13	4.19	3.81	4.85	0.28	NWR	13	4.07	3.23	4.80	0.41
PML	13	9.11	7.67	10.27	0.74	PML	13	8.62	7.99	10.23	0.75
UML	13	6.87	6.33	7.18	0.23	UML	13	6.65	6.23	7.01	0.29
HT-B	13	8.29	7.71	8.81	0.32	HT-B	13	8.08	7.68	8.52	0.26
BuL	13	4.19	3.62	4.50	0.26	BuL	13	4.02	3.76	4.28	0.16
I ¹ -P ³	13	10.00	9.43	10.45	0.28	I ¹ -P ³	13	9.54	8.88	10.12	0.37
LML	13	7.56	7.10	7.88	0.24	LML	13	7.33	6.96	7.71	0.29
I ₁ -P ₃	13	7.96	7.51	8.43	0.27	I ₁ -P ₃	13	7.57	7.09	8.03	0.36
M ₂ W	13	2.19	2.00	2.33	0.10	M ₂ W	13	2.09	1.94	2.22	0.08
UPL	13	4.44	4.16	5.08	0.25	UPL	13	4.20	3.86	4.45	0.19

example, has larger anterior palatal vacuities than any congener. Within *A. minimus*, the most discriminating morphological features are tv and R-LM³, with *A. minimus maritimus* tending to be shorter-tailed and broader-skulled than *A. minimus minimus*, although there is overlap in both characters for both sexes (Figs 11-12).

DFA and CVA

Discriminant Function Analysis (DFA) of *A. minimus* with members of the Dusky Antechinus complex indicated that 100% of females and males were clustered into both *A. minimus* taxa (*A. minimus minimus*, *A. minimus*

maritimus) and the five Dusky *Antechinus* taxon groups (*A. swainsonii*, *A. vandycki*, *A. mimetes mimetes*, *A. mimetes insulanus* and *A. arktos*) correctly (posterior probabilities all equal to 1.00, not shown), based on the Mahalanobis distance of each individual from the centroid of

TABLE 4. Univariate statistics: means, standard deviations and range minima and maxima of measured variables for *Antechinus vandycki*.

MALES					
	Valid N	Mean	Min	Max	St. Dev.
wt	6	73.08	46.30	92.80	16.87
hb	6	120.21	104.91	132.60	9.82
tv	6	109.06	92.34	118.02	9.39
hf	6	22.47	20.34	24.62	1.67
e	6	16.37	14.94	17.55	1.00
APV	7	7.22	7.05	7.48	0.18
BL	7	31.71	29.90	33.20	1.04
Dent	7	25.92	24.48	27.76	1.02
IBW	7	4.48	4.21	4.75	0.21
IOW	7	7.95	7.67	8.11	0.15
IPV	7	1.56	1.27	1.68	0.15
M ² W	7	2.33	2.24	2.38	0.05
NW	7	2.32	2.21	2.51	0.10
OBW	7	12.64	12.04	13.07	0.35
PPV	7	6.11	5.78	6.54	0.29
R-LC ¹	7	4.86	4.66	5.02	0.12
R-LM ¹	7	8.68	8.23	9.08	0.34
R-LM ¹ T	7	7.87	7.61	8.15	0.16
R-LM ²	7	10.55	9.70	10.97	0.47
R-LM ³	7	12.91	12.39	13.44	0.37
ZW	7	17.25	15.99	18.39	0.71
HT	7	10.72	10.36	11.32	0.30
PL	7	18.73	17.89	19.38	0.56
SWR-LC ¹ B	7	4.36	4.24	4.59	0.14
TC	7	2.66	2.44	2.88	0.18
NWR	7	4.44	4.18	4.87	0.24
PML	7	9.52	8.94	10.21	0.39
UML	7	6.94	6.78	7.08	0.11
HT-B	7	8.46	7.82	8.84	0.34
BuL	7	4.41	4.15	4.57	0.16
P ¹ -P ³	7	10.49	10.14	11.00	0.30
LML	7	7.58	7.37	7.68	0.11
I ₁ -P ₃	7	8.41	8.18	8.63	0.17
M ₂ W	7	2.21	2.17	2.27	0.04
UPL	7	4.66	4.45	4.79	0.11

the *a priori* species group. For CVA, 100% of the variation in dental characters was explained in the first six canonical roots for males and the first five roots for females. Variation was well resolved for both sexes, as eigenvalues for the first three canonical roots were well above 1 (males: root 1 = 43.9; root 2 = 8.9; root 3 = 2.5; females: root 1 = 40.1; root 2 = 22.8; root 3 = 5.7) and about three-quarters of the variation was explained in the first root (74%) for males, whereas just over half (56%) was explained in the first root for females. Further, cumulatively the first two roots explained 90% of variation in males and 88% in females. Figs 13-16 show scatterplots of canonical roots for males and Figs 17-18 for females; all species are tightly clustered within their taxon and well separated between species, for both sexes, but particularly females. However, there is some overlap between subspecies of *A. minimus*, particularly in males; canonical variates 4 and 5 (Figs 15-16) are important for discriminating the subspecies of *A. minimus* in males, whereas canonical variates 1 and 2 defined adjacent but distinct clusters of *A. minimus minimus* and *A. minimus maritimus*. The close and sometimes overlapping positions of the *A. minimus* subspecies in the multivariate analysis reflects the subtle morphological and only moderate genetic differences between them.

To facilitate direct comparison, univariate statistics (means, standard deviations, range minima and maxima) are shown for each of the external and internal (cranial/dental) measures for both subspecies of *A. minimus* and all four species (5 taxa) within the Dusky *Antechinus* species complex: *A. swainsonii*, *A. vandycki*, *A. mimetes mimetes*, *A. mimetes insulanus* and *A. arktos* (refer Tables 1-7). All ANOVAs of measured variables among all antechinus species were significant (Table 8). In pairwise comparisons below, attention is given to diagnosing absolute differences (with no overlap in ranges) where they exist, compared to those that are significantly ($P < 0.05$) different. *Antechinus minimus minimus*, with primacy of discovery within *A. minimus*, was chosen as the reference species, to which all other congeners are compared in pairwise fashion below.

Swamp Antechinus, *Antechinus minimus* (É. Geoffroy)

TABLE 5. Univariate statistics: means, standard deviations and range minima and maxima of measured variables for *Antechinus mimetes mimetes*.

MALES						FEMALES					
	Valid N	Mean	Min	Max	St. Dev.		Valid N	Mean	Min	Max	St. Dev.
wt	6	60.55	42.00	112.00	26.01	wt	8	38.24	30.50	47.80	5.10
hb	20	122.18	89.20	150.00	16.50	hb	27	106.14	85.00	125.00	11.59
tv	20	101.11	82.43	113.75	8.83	tv	27	89.53	76.00	98.00	5.77
hf	20	21.41	18.69	24.00	1.41	hf	26	19.61	17.00	22.00	1.15
e	19	16.56	14.29	20.00	1.63	e	26	15.82	14.08	19.40	1.18
APV	15	5.41	4.58	6.35	0.52	APV	12	5.02	4.57	5.56	0.28
BL	15	30.39	28.53	31.72	0.93	BL	11	28.63	27.33	30.49	0.98
Dent	15	24.67	23.21	25.88	0.79	Dent	12	23.18	22.05	24.30	0.74
IBW	15	4.73	4.35	5.12	0.24	IBW	12	4.46	4.05	4.87	0.25
IOW	15	8.12	7.68	8.51	0.23	IOW	12	7.85	7.21	8.34	0.33
IPV	15	3.19	2.13	3.93	0.60	IPV	12	3.09	2.43	3.79	0.42
M ² W	15	2.36	2.20	2.53	0.09	M ² W	12	2.25	2.10	2.37	0.07
NW	15	2.70	2.41	2.92	0.15	NW	12	2.54	2.14	3.02	0.24
OBW	15	12.34	11.60	13.33	0.50	OBW	12	11.85	11.11	12.53	0.40
PPV	15	5.41	4.37	6.03	0.48	PPV	12	5.29	4.67	5.71	0.26
R-LC ¹	15	4.63	4.34	4.92	0.19	R-LC ¹	12	4.34	3.79	4.71	0.26
R-LM ¹	15	8.78	8.03	9.39	0.38	R-LM ¹	12	8.45	7.68	8.93	0.38
R-LM ¹ T	15	7.68	7.27	8.15	0.29	R-LM ¹ T	12	7.34	6.80	7.63	0.28
R-LM ²	15	10.65	9.63	11.81	0.62	R-LM ²	12	10.24	9.09	11.06	0.68
R-LM ³	15	13.28	12.23	14.39	0.56	R-LM ³	12	12.78	11.15	13.64	0.71
ZW	15	17.00	15.52	18.07	0.77	ZW	12	15.74	14.47	16.94	0.76
HT	15	10.76	10.28	11.15	0.28	HT	12	10.34	9.81	10.92	0.32
PL	15	17.51	16.66	18.27	0.51	PL	12	16.77	15.83	17.69	0.53
SWR-LC ¹ B	15	4.18	3.78	4.63	0.22	SWR-LC ¹ B	12	3.88	3.47	4.29	0.28
TC	15	2.90	2.50	3.41	0.29	TC	12	2.83	2.54	3.36	0.26
NWR	15	4.62	4.12	4.87	0.23	NWR	12	4.23	3.67	4.68	0.37
PML	15	9.39	8.21	10.70	0.69	PML	12	8.60	7.84	9.47	0.54
UML	15	6.93	6.29	7.52	0.34	UML	12	6.72	6.25	7.17	0.26
HT-B	15	8.57	8.21	9.04	0.24	HT-B	12	8.16	7.57	8.55	0.31
BuL	15	4.26	3.93	4.60	0.21	BuL	12	4.06	3.82	4.33	0.18
I ¹ -P ³	15	9.67	8.98	10.20	0.33	I ¹ -P ³	12	9.16	8.82	9.90	0.29
LML	15	7.60	7.00	8.19	0.37	LML	12	7.37	6.87	7.73	0.26
I ₁ -P ₃	15	7.78	7.31	8.08	0.26	I ₁ -P ₃	12	7.30	6.93	7.75	0.23
M ₂ W	15	2.18	1.98	2.41	0.12	M ₂ W	12	2.13	2.00	2.25	0.08
UPL	15	4.38	4.03	4.70	0.23	UPL	12	4.09	3.61	4.52	0.26

Antechinus minimus minimus (Geoffroy)
versus

Antechinus minimus maritimus (Finlayson)

Pelage. *Antechinus minimus minimus* and *A. minimus maritimus* are similar in appearance, with coarse fur and a leaden grey head that

merges to brownish yellow fur on the rump and flanks.

External Measurements. *Antechinus minimus minimus* is similar in size compared to *A. minimus maritimus*, although *A. minimus minimus* tends to

TABLE 6. Univariate statistics: means, standard deviations and range minima and maxima of measured variables for *Antechinus mimetes insulanus*.

MALES						FEMALES					
	Valid N	Mean	Min	Max	St. Dev.		Valid N	Mean	Min	Max	St. Dev.
wt	4	70.63	46.00	87.00	17.55	wt	4	49.75	40.00	60.00	8.26
hb	6	138.87	117.10	165.00	17.48	hb	6	123.20	111.40	144.80	11.35
tv	6	111.86	105.00	121.90	7.62	tv	5	99.49	96.39	106.27	3.88
hf	6	22.04	20.00	24.26	1.49	hf	6	20.50	19.60	21.27	0.60
e	5	17.47	15.45	20.50	1.92	e	6	17.02	14.00	19.40	2.00
APV	6	5.63	5.06	6.02	0.33	APV	11	5.16	4.72	5.50	0.27
BL	6	32.57	30.19	33.85	1.37	BL	11	29.93	28.39	30.74	0.71
Dent	6	26.53	24.68	27.61	1.07	Dent	11	24.37	22.96	25.03	0.56
IBW	6	5.14	4.99	5.34	0.14	IBW	11	4.77	4.55	4.99	0.15
IOW	6	7.94	7.78	8.27	0.17	IOW	11	7.86	7.59	8.08	0.14
IPV	6	3.88	3.48	4.24	0.26	IPV	11	3.82	3.41	4.23	0.24
M ² W	6	2.58	2.53	2.65	0.05	M ² W	11	2.50	2.44	2.54	0.03
NW	6	2.93	2.77	3.19	0.16	NW	11	2.90	2.61	3.12	0.14
OBW	6	13.41	12.98	13.85	0.35	OBW	11	12.56	11.99	13.33	0.37
PPV	6	5.31	4.60	5.57	0.36	PPV	11	4.92	4.34	5.43	0.36
R-LC ¹	6	4.99	4.71	5.26	0.22	R-LC ¹	11	4.61	4.32	4.92	0.19
R-LM ¹	6	9.07	8.86	9.31	0.16	R-LM ¹	11	8.53	8.08	8.78	0.23
R-LM ¹ T	6	8.29	8.01	8.76	0.27	R-LM ¹ T	11	7.92	7.60	8.24	0.19
R-LM ²	6	10.61	10.12	11.43	0.53	R-LM ²	11	9.91	9.28	10.50	0.39
R-LM ³	6	14.09	13.85	14.45	0.23	R-LM ³	11	13.12	12.43	13.86	0.47
ZW	6	18.80	17.83	20.01	0.83	ZW	11	17.09	16.48	17.90	0.47
HT	6	11.20	10.65	11.89	0.46	HT	11	10.66	10.27	10.89	0.21
PL	6	18.84	17.88	19.36	0.53	PL	11	17.78	16.84	18.16	0.43
SWR-LC ¹ B	6	4.47	4.22	4.74	0.21	SWR-LC ¹ B	11	4.10	3.85	4.34	0.16
TC	6	3.11	2.96	3.28	0.14	TC	11	3.07	2.71	3.39	0.22
NWR	6	5.11	4.82	5.41	0.23	NWR	11	4.73	4.44	5.19	0.22
PML	6	10.64	9.90	11.30	0.47	PML	11	9.63	8.84	10.20	0.43
UML	6	7.46	7.35	7.62	0.11	UML	11	7.20	6.96	7.37	0.14
HT-B	6	8.97	8.49	9.48	0.36	HT-B	11	8.30	8.00	8.58	0.18
BuL	6	4.43	4.19	4.73	0.19	BuL	11	4.24	3.99	4.68	0.22
I ¹ -P ³	6	10.20	9.42	10.61	0.43	I ¹ -P ³	11	9.54	9.19	9.90	0.25
LML	6	8.13	8.00	8.43	0.17	LML	11	7.91	7.67	8.08	0.13
I ₁ -P ₃	6	8.33	7.89	8.65	0.31	I ₁ -P ₃	11	7.59	7.18	7.82	0.21
M ₂ W	6	2.36	2.33	2.43	0.04	M ₂ W	11	2.30	2.24	2.34	0.03
UPL	6	4.55	4.13	4.91	0.29	UPL	11	4.18	3.91	4.57	0.20

have larger hind feet and a longer tail (Tables 1, 2 and 8).

Craniodental Characters. *Antechinus minimus minimus* is not significantly different to *A. minimus maritimus* for any craniodental characters, but *A. minimus minimus* tend to have a narrower skull

(smaller R-LM¹T, R-LM², R-LM³) in both sexes and narrower M²W in females (Tables 1, 2 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. minimus maritimus* is found on mainland Australia (as

Swamp Antechinus, *Antechinus minimus* (É. Geoffroy)

TABLE 7. Univariate statistics: means, standard deviations and range minima and maxima of measured variables for *Antechinus arktos*.

MALES						FEMALES					
	Valid N	Mean	Min	Max	St. Dev.		Valid N	Mean	Min	Max	St. Dev.
wt	2	89.85	59.70	120.00	42.64	wt	1	46.30	46.30	46.30	na
hb	5	131.53	108.58	145.00	14.91	hb	3	108.89	106.22	111.20	2.51
tv	6	118.01	100.42	131.00	14.22	tv	3	99.12	94.20	106.88	6.80
hf	6	23.27	21.88	24.00	0.80	hf	3	21.43	20.00	22.20	1.24
e	6	17.15	15.47	19.00	1.39	e	3	16.70	16.10	17.72	0.89
APV	6	4.76	4.52	5.05	0.22	APV	3	4.45	4.31	4.64	0.17
BL	6	32.44	30.45	33.75	1.55	BL	3	29.54	29.12	30.14	0.53
Dent	6	26.31	24.63	27.41	1.16	Dent	3	24.30	24.14	24.51	0.19
IBW	6	5.08	4.93	5.23	0.13	IBW	3	4.68	4.53	4.83	0.15
IOW	6	8.05	7.87	8.51	0.24	IOW	3	7.94	7.78	8.13	0.18
IPV	6	4.11	3.97	4.24	0.12	IPV	3	4.05	3.94	4.13	0.10
M ² W	6	2.41	2.35	2.52	0.06	M ² W	3	2.40	2.35	2.43	0.04
NW	6	3.15	2.99	3.43	0.16	NW	3	2.90	2.76	3.02	0.13
OBW	6	13.21	12.63	13.72	0.41	OBW	3	12.38	12.32	12.46	0.07
PPV	6	5.85	5.02	6.52	0.57	PPV	3	5.56	5.45	5.76	0.17
R-LC ¹	6	5.10	4.93	5.31	0.16	R-LC ¹	3	4.68	4.62	4.72	0.05
R-LM ¹	6	9.57	9.12	9.90	0.29	R-LM ¹	3	8.74	8.66	8.79	0.07
R-LM ^{1T}	6	8.15	7.97	8.29	0.14	R-LM ^{1T}	3	7.77	7.71	7.82	0.06
R-LM ²	6	11.42	10.95	11.65	0.27	R-LM ²	3	10.60	10.51	10.68	0.09
R-LM ³	6	14.09	13.55	14.70	0.42	R-LM ³	3	13.29	13.01	13.47	0.25
ZW	6	18.27	16.65	19.22	1.20	ZW	3	16.61	16.27	17.10	0.43
HT	6	10.95	10.55	11.38	0.27	HT	3	10.60	10.56	10.64	0.04
PL	6	18.38	17.45	19.04	0.61	PL	3	17.45	17.26	17.71	0.23
SWR-LC ¹ B	6	4.60	4.33	5.03	0.25	SWR-LC ¹ B	3	4.09	4.03	4.13	0.05
TC	6	3.22	2.97	3.38	0.15	TC	3	3.14	3.03	3.33	0.17
NWR	6	5.75	5.22	6.17	0.37	NWR	3	4.99	4.82	5.32	0.29
PML	6	10.23	9.68	10.78	0.44	PML	3	9.57	9.37	9.85	0.25
UML	6	7.35	7.21	7.55	0.11	UML	3	7.33	7.19	7.46	0.14
HT-B	6	8.76	8.53	9.08	0.20	HT-B	3	8.35	8.10	8.48	0.22
BuL	6	4.57	4.25	4.79	0.21	BuL	3	4.48	4.37	4.55	0.09
I ¹ -P ³	6	10.03	9.58	10.29	0.26	I ¹ -P ³	3	9.48	9.32	9.66	0.17
LML	6	7.83	7.72	8.07	0.12	LML	3	7.74	7.57	7.92	0.18
I ₁ -P ₃	6	7.99	7.16	8.36	0.44	I ₁ -P ₃	3	7.35	6.98	7.68	0.35
M ₂ W	6	2.27	2.13	2.35	0.08	M ₂ W	3	2.28	2.20	2.35	0.08
UPL	6	4.50	4.29	4.71	0.17	UPL	3	4.15	3.99	4.24	0.14

well as some near-coastal islands) and is patchily distributed in mostly coastal areas between South Gippsland (Victoria) and Robe (South Australia). Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. minimus uarittimus* is 3.9 - 4.5%.

Antechinus minimus minimus versus *Antechinus swainsonii* (Waterhouse)

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. swainsonii* is greyish-brown in

TABLE 8. ANOVA F-statistics (top two lines) for variation at each of the measured variables among all antechinus species and subspecies. Subsequent rows show significance values for ANOVA post-hoc tests of *Antechinus minimus minimus* paired with each of its 14 congeneric species, for each measured variable. Shaded cells are significant at $p=0.05$, unshaded cells are not significant.

Comparison	sex	wt	hb	tv	hf	e	APV	BL	Dent	IBW	IOW	IPV	MAW	NIV	OBW	PPV	R-IC1	R-IM1	R-LM1T	
ANOVA F - all species	male	22.90	29.66	37.28	50.49	21.31	235.90	41.94	48.85	37.85	86.90	90.51	58.12	29.49	24.38	21.61	50.91	46.38	29.76	
ANOVA F - all species	female	26.69	24.47	25.22	29.42	19.61	219.10	48.39	65.25	39.25	97.35	74.40	51.69	19.39	28.13	18.55	43.46	44.46	25.68	
<i>minimus maritimus</i>	male	1.00	0.99	0.68	0.29	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.87	0.90
<i>minimus maritimus</i>	female	0.99	1.00	0.42	0.91	1.00	0.96	1.00	1.00	1.00	1.00	0.85	0.14	1.00	1.00	1.00	1.00	1.00	1.00	0.74
<i>swainsonii</i>	male	0.96	1.00	0.02	0.81	0.05	0.00	0.06	0.01	1.00	0.98	0.00	1.00	0.04	1.00	0.97	0.00	0.03	0.99	
<i>swainsonii</i>	female	1.00	1.00	0.00	0.84	0.23	0.00	0.00	0.01	1.00	0.03	0.00	0.95	0.16	1.00	0.99	0.01	0.89	1.00	
<i>tombacki</i>	male	1.00	0.98	0.00	0.82	0.94	0.00	0.00	0.00	1.00	1.00	0.00	1.00	0.02	1.00	0.00	0.68	0.93	1.00	
<i>minimetus mimetes</i>	male	1.00	0.95	0.00	0.33	0.20	0.00	0.02	0.00	1.00	0.04	0.00	0.46	1.00	1.00	0.69	0.00	0.84	1.00	
<i>minimetus mimetes</i>	female	0.98	0.97	0.00	0.18	0.00	0.00	0.00	0.01	1.00	0.00	0.93	0.24	0.90	0.99	0.12	0.16	1.00	1.00	
<i>minimetus insulanus</i>	male	1.00	1.00	0.00	0.16	0.23	0.00	0.00	0.00	0.06	1.00	1.00	0.00	0.99	0.00	1.00	1.00	1.00	0.47	
<i>minimetus insulanus</i>	female	0.48	0.80	0.00	0.06	0.00	0.00	0.00	0.01	0.00	0.02	0.65	0.00	0.61	0.00	1.00	1.00	1.00	0.00	
<i>arktos</i>	male	1.00	1.00	0.00	0.00	0.30	0.00	0.00	0.00	0.18	0.94	1.00	0.30	0.10	0.09	0.10	1.00	1.00	0.94	
<i>arktos</i>	female	1.00	1.00	0.00	0.04	0.19	0.00	0.00	0.01	0.95	0.52	0.88	0.03	1.00	0.41	0.44	1.00	1.00	0.95	
<i>adustus</i>	male	0.00	0.00	0.00	0.99	1.00	0.00	0.01	0.00	0.99	0.00	1.00	0.04	1.00	0.26	1.00	1.00	1.00	1.00	
<i>adustus</i>	female	0.00	0.00	0.00	1.00	0.87	0.00	0.80	0.21	1.00	0.00	0.27	0.00	1.00	0.18	1.00	0.71	1.00	1.00	
<i>agilis</i>	male	0.00	0.00	0.02	0.01	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.55	1.00	0.00	0.00	0.04	0.20	0.00	
<i>agilis</i>	female	0.00	0.00	0.39	0.02	1.00	0.00	0.03	0.00	0.00	0.00	0.81	0.51	0.28	0.17	0.41	1.00	1.00	1.00	
<i>argenteus</i>	male	0.00	0.00	0.40	0.81	0.57	0.00	0.45	0.07	0.02	0.00	1.00	1.00	1.00	1.00	0.88	1.00	0.99	1.00	
<i>argenteus</i>	female	0.02	0.00	1.00	0.64	0.90	0.01	0.39	0.21	0.02	0.00	1.00	0.68	1.00	1.00	0.21	1.00	1.00	1.00	
<i>bellus</i>	male	0.12	1.00	0.00	0.00	0.00	0.00	0.07	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>bellus</i>	female	0.46	1.00	0.00	0.01	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.22	0.00	0.01	
<i>flavipes flavipes</i>	male	0.00	0.00	0.81	0.89	0.21	0.00	1.00	0.87	0.00	0.00	0.00	0.00	1.00	0.66	0.13	0.00	0.84	0.00	
<i>flavipes flavipes</i>	female	0.98	0.00	0.95	0.54	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	
<i>flavipes leucogaster</i>	male	0.00	0.00	1.00	0.87	0.06	0.00	0.93	0.59	0.00	0.00	0.00	0.00	0.26	0.91	0.15	0.16	0.01	0.22	
<i>flavipes leucogaster</i>	female	0.04	0.00	1.00	0.41	0.00	0.00	1.00	1.00	0.00	0.67	0.00	0.00	0.88	1.00	0.37	0.51	0.01	0.08	
<i>flavipes rubecula</i>	male	1.00	0.99	0.00	0.19	0.16	0.00	0.51	0.10	0.78	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	
<i>flavipes rubecula</i>	female	1.00	1.00	0.00	0.53	0.92	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.75	0.00	0.00	0.00	
<i>godmani</i>	male	0.21	0.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.98	0.00	0.32	0.00	0.04	0.00	
<i>godmani</i>	female	0.00	0.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.70	0.00	0.11	0.00	
<i>leo</i>	male	1.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	
<i>leo</i>	female	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	
<i>mysticinus</i>	male	0.00	0.00	0.00	0.04	0.26	0.00	1.00	0.31	0.00	0.00	1.00	0.00	1.00	1.00	1.00	0.04	1.00	0.90	
<i>mysticinus</i>	female	0.00	0.00	0.06	0.26	0.00	0.00	1.00	0.60	0.00	0.00	0.76	0.00	1.00	1.00	1.00	0.00	1.00	0.61	
<i>stuartii</i>	male	0.00	0.00	0.64	0.01	0.59	0.00	0.00	0.00	0.00	0.00	0.00	0.69	1.00	0.08	0.69	0.95	0.53	1.00	
<i>stuartii</i>	female	0.00	0.00	1.00	0.31	0.46	0.00	0.03	0.00	0.00	0.00	0.86	0.04	0.50	0.30	0.10	1.00	1.00	0.23	
<i>subtropicus</i>	male	0.13	0.37	0.10	1.00	0.00	0.97	1.00	0.98	0.03	0.00	0.00	0.00	0.00	1.00	0.00	1.00	1.00	1.00	
<i>subtropicus</i>	female	0.58	0.00	0.50	1.00	0.17	1.00	1.00	1.00	0.20	0.00	0.00	0.00	1.00	1.00	0.00	0.91	1.00	0.77	

Swamp Antechinus, *Antechinus minimus* (E. Geoffroy)

TABLE 8. cont ...

Comparison	sex	R-LMF	R-LMP	ZW	HT	PL	SWR-LCB	TC	NWR	PML	UML	HT-B	BuL	U-P3	LML	I ₁ -P ₃	M ₂ W	UPL
ANOVA F - all species	male	45.96	29.84	16.46	35.27	63.05	42.04	27.23	14.61	20.45	55.11	40.40	23.95	78.64	56.11	127.60	40.06	90.44
ANOVA F - all species	female	47.29	29.48	20.11	52.35	74.68	38.58	31.24	14.46	28.72	56.33	59.21	24.64	46.45	59.31	121.10	49.32	90.68
<i>minimus maritimus</i>	male	0.30	0.37	1.00	1.00	1.00	0.98	0.82	1.00	0.94	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>minimus maritimus</i>	female	0.66	0.54	1.00	1.00	1.00	0.98	1.00	1.00	0.69	0.79	1.00	0.56	1.00	0.11	0.95	0.88	1.00
<i>swainsonii</i>	male	0.92	1.00	1.00	1.00	0.00	0.00	0.00	0.30	1.00	0.00	0.94	1.00	0.00	0.00	0.00	0.01	0.00
<i>swainsonii</i>	female	0.99	1.00	1.00	1.00	0.00	0.36	1.00	0.99	0.03	0.00	1.00	0.79	0.00	0.00	0.00	0.84	0.00
<i>vandycki</i>	male	1.00	1.00	1.00	1.00	0.00	1.00	0.69	1.00	0.68	0.00	1.00	0.85	0.00	0.00	0.00	0.06	0.00
<i>nimetus nimetus</i>	male	1.00	1.00	1.00	1.00	0.00	0.00	1.00	1.00	0.39	0.00	1.00	1.00	0.00	0.00	0.00	0.01	0.00
<i>nimetus nimetus</i>	female	1.00	0.78	0.95	0.96	0.00	0.96	0.99	1.00	0.04	0.00	1.00	0.48	0.00	0.00	0.00	0.03	0.00
<i>nimetus insulanus</i>	female	0.90	0.08	0.00	0.00	0.00	1.00	0.00	0.58	0.00	0.00	0.75	0.00	0.00	0.00	0.00	0.00	0.00
<i>arkhis</i>	male	0.96	0.35	0.46	1.00	0.00	1.00	0.62	0.00	0.00	0.00	0.99	0.10	0.00	0.00	0.00	0.00	0.00
<i>arkhis</i>	female	1.00	0.73	0.52	0.87	0.00	1.00	0.27	0.78	0.00	0.00	0.99	0.00	0.14	0.00	0.00	0.00	0.00
<i>adustus</i>	male	1.00	1.00	0.87	0.00	0.00	1.00	0.67	1.00	0.00	1.00	0.00	0.17	0.00	1.00	0.00	0.00	0.00
<i>adustus</i>	female	1.00	1.00	1.00	0.00	0.10	0.34	1.00	0.92	0.00	1.00	0.00	0.80	0.03	1.00	0.00	0.00	0.00
<i>agilis</i>	male	1.00	1.00	0.09	0.00	0.00	0.62	0.00	0.00	0.00	0.00	0.00	0.97	0.00	0.00	0.00	0.94	0.00
<i>agilis</i>	female	0.12	0.43	1.00	0.00	0.00	1.00	0.90	0.00	1.00	0.90	0.00	0.40	0.00	0.95	0.00	1.00	0.00
<i>argenteus</i>	male	0.14	0.46	1.00	0.00	0.02	1.00	0.39	0.27	1.00	1.00	0.00	1.00	0.00	1.00	0.00	0.92	0.00
<i>argenteus</i>	female	1.00	0.91	1.00	0.00	0.15	1.00	1.00	0.20	1.00	1.00	0.00	0.76	0.14	1.00	0.00	0.98	0.00
<i>bellus</i>	male	0.00	0.00	0.00	0.96	0.15	0.00	0.00	0.28	1.00	0.00	0.00	0.00	0.99	0.00	0.00	0.00	0.14
<i>bellus</i>	female	0.00	0.00	0.00	0.99	0.26	0.00	0.17	0.20	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.04
<i>flavipes flavipes</i>	male	0.00	0.00	0.44	0.00	0.76	0.00	0.00	0.44	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>flavipes flavipes</i>	female	0.00	0.00	0.11	0.00	0.96	0.00	0.04	0.04	0.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>flavipes leucogaster</i>	male	0.00	0.00	0.78	0.00	0.00	0.09	0.04	0.00	0.94	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
<i>flavipes leucogaster</i>	female	0.00	0.00	0.13	0.00	0.38	0.00	0.98	0.05	0.95	1.00	0.00	0.00	0.03	1.00	0.00	0.00	0.00
<i>flavipes ruberulus</i>	male	0.00	0.00	0.00	0.41	0.76	0.00	0.25	1.00	0.13	0.00	0.00	0.00	0.75	0.00	0.00	0.00	0.02
<i>flavipes ruberulus</i>	female	0.00	0.00	0.00	0.98	0.00	0.00	1.00	1.00	0.18	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.08
<i>goldmani</i>	male	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.62	0.00	1.00	0.81	0.00	0.00	0.46	0.00	0.00
<i>goldmani</i>	female	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.99	0.01	0.00	0.00	0.00	0.00	0.00
<i>leo</i>	male	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.03	0.00	0.00	0.16	0.00	1.00	0.00	0.00	0.00	0.99
<i>leo</i>	female	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.38	0.00	0.00	0.01	0.00	0.98	0.00	0.11	0.00	1.00
<i>mysticus</i>	male	0.85	0.04	1.00	0.00	0.24	0.00	0.00	0.81	1.00	1.00	0.00	0.15	0.00	1.00	0.00	0.29	0.00
<i>mysticus</i>	female	0.55	0.20	0.88	0.00	0.18	0.00	1.00	0.89	1.00	1.00	0.00	0.00	0.00	1.00	0.00	0.11	0.00
<i>stuartii</i>	male	0.98	1.00	0.48	0.00	0.00	1.00	0.35	0.00	0.06	1.00	0.00	1.00	0.00	1.00	0.00	0.04	0.00
<i>stuartii</i>	female	0.98	1.00	1.00	0.00	0.00	1.00	0.93	0.00	0.59	1.00	0.00	1.00	0.00	1.00	0.00	0.04	0.00
<i>subtropicus</i>	male	1.00	1.00	1.00	0.00	0.88	0.93	1.00	0.05	1.00	0.95	0.00	1.00	0.00	0.92	0.00	0.00	0.00
<i>subtropicus</i>	female	1.00	1.00	1.00	0.00	1.00	0.04	1.00	0.49	1.00	0.38	0.00	0.78	0.93	0.05	0.00	0.00	0.00

appearance, greyer at the front with a brownish warming on the rump.

External Measurements. *Antechinus minimus minimus* is significantly smaller than *A. swainsonii* in tv and hf length in males and for tv length in females (Tables 1, 3 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. swainsonii* in absolute measurement (i.e., with no overlap) for IPV in males and females. *Antechinus minimus minimus* is significantly larger than *A. swainsonii* in NW, R-LC¹, R-LM¹, SWR-LC¹B and TC in males and for R-LC¹ in females. *Antechinus minimus minimus* is smaller than *A. swainsonii* in absolute measurement for APV in both sexes and for UPL in males. *Antechinus minimus minimus* is significantly smaller than *A. swainsonii* in Dent, PL, UML, I¹-P³, LML, I₁-P₃ and M₂W in males and for BL, Dent, IOW, PL, PML, UML, I¹-P³, LML, I₁-P₃ and UPL in females (Tables 1, 3 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) and may co-occur with *A. swainsonii*, which occurs throughout much of Tasmania, except the far south-east on Tasman Peninsula. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. swainsonii* is 10.0 – 12.0%.

Antechinus minimus minimus versus
Antechinus vandycki Baker,
Mutton, Mason and Gray

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. vandycki* is dark greyish-brown in appearance, greyer at the front with a brownish warming on the rump.

External Measurements. *Antechinus minimus minimus* is significantly smaller than *A. vandycki* in tv and hf length in males (Tables 1, 4 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. vandycki* in absolute measurement for IPV in males. *Antechinus minimus minimus* is significantly larger than *A.*

vandycki in NW for males. *Antechinus minimus minimus* is smaller than *A. vandycki* in absolute measurement for APV, PL, I¹-P³, LML, I₁-P₃ and UPL in males. *Antechinus minimus minimus* is significantly smaller than *A. vandycki* in BL, Dent, PPV and UML in males (Tables 1, 4 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. vandycki* occurs only in the far south-east on Tasman Peninsula. The two species may co-occur on Tasman Peninsula. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. vandycki* is 9.4-10.2%.

Antechinus minimus minimus versus
Antechinus mimetes mimetes (Thomas)

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. mimetes mimetes* is more evenly brownish from head to rump.

External Measurements. *Antechinus minimus minimus* is significantly smaller than *A. mimetes mimetes* in tv for males and for tv and e in females (Tables 1, 5 and 8).

Craniodental Characters. *Antechinus minimus minimus* is significantly larger than *A. mimetes mimetes* in IPV, R-LC¹ and SWR-LC¹B for males. *Antechinus minimus minimus* is smaller than *A. mimetes mimetes* in absolute measurement for APV in males and females and for I¹-P³ in females. *Antechinus minimus minimus* is significantly smaller than *A. mimetes mimetes* in BL, Dent, IOW, PL, UML, I¹-P³, LML, I₁-P₃, M₂W and UPL for males and for BL, Dent, IOW, PL, PML, UML, LML, I₁-P₃, M₂W and UPL for females (Tables 1, 5 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. mimetes mimetes* is found on mainland Australia in Victoria and New South Wales. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. mimetes mimetes* is 8.6-10.6%.

Antechinus minimus minimus versus
Antechinus mimetes insulanus Davison

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. mimetes insulanus* is more evenly brownish from head to rump.

External Measurements. *Antechinus minimus minimus* is smaller than *A. mimetes insulanus* in absolute measurement (i.e., with no overlap) for tv in males and females. *Antechinus minimus minimus* is significantly smaller than *A. mimetes insulanus* in e for females (Tables 1, 6 and 8).

Craniodontal Characters. *Antechinus minimus minimus* is smaller than *A. mimetes insulanus* in absolute measurement for APV, M²W, OBW, PL, PML, UML, LML, I₁-P₃ and M₂W in males and for APV, BL, Dent, M²W, ZW, PL, PML, UML, I¹-P³, LML, I₁-P₃, M₂W and UPL in females. *Antechinus minimus minimus* is significantly smaller than *A. mimetes insulanus* in BL, Dent, ZW, I₁-P₃ and UPL for males and for IBW, IOW, OBW, R-LM¹T, HT, TC and BuL for females (Tables 1, 6 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. mimetes insulanus* is found on mainland Australia in the Grampians NP, Victoria. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. mimetes insulanus* is 9.2-9.6%.

Antechinus minimus minimus versus
Antechinus arktos Baker, Mutton,
Hines & Van Dyck

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. arktos* is more brownish from head to rump with a very warm orangish rump and some orange fur around the eye.

External Measurements. *Antechinus minimus minimus* is smaller than *A. arktos* in absolute measurement for tv in males and females. *Antechinus minimus minimus* is significantly

smaller than *A. arktos* in hf for males and females (Tables 1, 7 and 8).

Craniodontal Characters. *Antechinus minimus minimus* is smaller than *A. arktos* in absolute measurement for APV, PML, UML, LML and UPL for males and for APV, BL, Dent, M²W, PL, PML, UML, BuL, I¹-P³, LML, M₂W and UPL in females. *Antechinus minimus minimus* is significantly smaller than *A. arktos* in BL, Dent, PL, NWR, I¹-P³, I₁-P₃ and M₂W in males and for I₁-P₃ in females (Tables 1, 7 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. arktos* is found on the border of Qld and NSW in the Tweed Volcano Caldera. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. arktos* is 9.2-10.4%.

Antechinus minimus minimus versus
Antechinus adustus (Thomas)

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. adustus* has more uniformly dark brown fur with rusty tips on the head and back.

External Measurements. *Antechinus minimus minimus* is larger than *A. adustus* in absolute measurement for hb in females. *Antechinus minimus minimus* is significantly larger than *A. adustus* in wt and hb in males and for wt in females (Tables 1 and 8).

Craniodontal Characters. *Antechinus minimus minimus* is larger than *A. adustus* in absolute measurement for APV, IOW, HT, HT-B, I₁-P₃ in both sexes and for I¹-P³ in females only. *Antechinus minimus minimus* is significantly larger than *A. adustus* in BL, Dent, PL, PML, I¹-P³ and UPL for males and for PML and UPL in females. *Antechinus minimus minimus* is smaller than *A. adustus* in absolute measurement for M²W in females. *Antechinus minimus minimus* is significantly smaller than *A. adustus* in M²W and M₂W in males and for M₂W in females (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. adustus* is found in the wet tropics of north-east Qld. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. adustus* is 14.3-15.7%.

Antechinus minimus minimus versus
Antechinus agilis Dickman,
Parnaby, Crowther and King

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. agilis* is a uniform medium grey to greyish brown from head to rump.

External Measurements. *Antechinus minimus minimus* is larger than *A. agilis* in absolute measurement for hb in females. *Antechinus minimus minimus* is significantly larger than *A. agilis* in wt, hb and hf in males and for wt and hf in females. *Antechinus minimus minimus* is significantly smaller than *A. agilis* in tv for males (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. agilis* in absolute measurement for APV, PL, HT-B, I₁-P₃ in males and for APV, IBW, IOW, HT, NWR, HT-B, I₁-P₃, I₁-P₃ and UPL in females. *Antechinus minimus minimus* is significantly larger than *A. agilis* in BL, Dent, IBW, IOW, OBW, PPV, R-LC₁, R-LM₁T, HT, TC, NWR, PML, UML, I₁-P₃, I₁-P₃, LML and UPL in males and for BL, Dent and PL in females (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. agilis* is known only from south-eastern Australia, south of around Sydney's (NSW) latitude. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. agilis* is 14.3-15.5%.

Antechinus minimus minimus versus
Antechinus argentus Baker,
Mutton and Hines

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. argentus* has a silvery head and neck that merge subtly to deep olive-buff coloured fur on the rump and flanks.

External Measurements. *Antechinus minimus minimus* is larger than *A. argentus* in absolute measurement for hb in males and for wt and hb in females. *Antechinus minimus minimus* is significantly larger than *A. argentus* in wt for males (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. argentus* in absolute measurement for APV, IOW, HT, PL, HT-B, I₁-P₃, I₁-P₃ for males and for APV, IOW, HT, HT-B, I₁-P₃ and UPL in females. *Antechinus minimus minimus* is significantly larger than *A. argentus* in IBW for both sexes and for UPL in males only (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. argentus* is known only from Kroombit Tops NP in south-east Qld. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. argentus* is 14.1-14.7%.

Antechinus minimus minimus versus
Antechinus bellus (Thomas)

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. bellus* is pale to medium grey above, sometimes with a fawn tinge, with pale grey belly, hands and feet.

External Measurements. *Antechinus minimus minimus* is smaller than *A. bellus* in absolute measurement for tv and e in males and for e in females. *Antechinus minimus minimus* is significantly smaller than *A. bellus* in hf for males and for tv and hf in females (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. bellus* in absolute measurement for APV and IOW in males and for IBW, IOW and PPV in females. *Antechinus minimus minimus* is significantly larger than *A. bellus* in IBW, PPV, TC, HT-B and I₁-P₃ in males and for APV, HT-B, I₁-P₃ and UPL in females. *Antechinus minimus minimus* is smaller than *A. bellus* in absolute measurement for IPV, M²W, R-LC¹, R-LM¹, R-LM², R-LM³, SWR-LC¹B, BuL and M₂W in males and for IPV, M²W, R-LC¹, R-LM¹, R-LM², R-LM³, SWR-LC¹B, UML, BuL, LML and M₂W in females. *Antechinus minimus minimus* is significantly smaller than *A. bellus* in NW, OBW, R-LM¹T, ZW, UML and LML in males and for BL, NW, OBW, R-LM¹T and ZW in females (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. bellus* is known only from northern Northern Territory. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. bellus* is 13.8-14.5%.

Antechinus minimus minimus versus
Antechinus flavipes flavipes (Waterhouse)

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. flavipes flavipes* has a similarly coloured head and rump but with marked orange-tonings on the hands, feet and tail base as well as a pale eye ring.

External Measurements. *Antechinus minimus minimus* is significantly larger than *A. flavipes flavipes* for wt and hb in males and hb in females. *Antechinus minimus minimus* is significantly smaller than *A. flavipes flavipes* in e for females (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. flavipes flavipes* in absolute measurement for IOW and I₁-P₃ for males and for APV, IOW, I₁-P₃ and UPL for females. *Antechinus minimus minimus* is significantly larger than *A. flavipes flavipes* in APV, IBW, HT, TC, HT-B, I¹-P³ and UPL for males and for IBW, HT, TC, NWR, HT-B and

I¹-P³ in females. *Antechinus minimus minimus* is smaller than *A. flavipes flavipes* in absolute measurement for M²W and M₂W in both sexes. *Antechinus minimus minimus* is significantly smaller than *A. flavipes flavipes* in IPV, NW, R-LC¹, R-LM¹, R-LM¹T, R-LM², R-LM³, SWR-LC¹B, UML, BuL and LML in males and for IPV, R-LC¹, R-LM¹T, R-LM², R-LM³, SWR-LC¹B, UML, BuL and LML in females (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. flavipes flavipes* occurs in a wide range of drier habitat in mainland south-east Australia. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. flavipes flavipes* is 15.1-16.5%.

Antechinus minimus minimus versus
Antechinus flavipes leucogaster Gray

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. flavipes leucogaster* has a similarly coloured head and rump but with yellowish-brown fur on the hands, feet and tail base and a pale eyering.

External Measurements. *Antechinus minimus minimus* is significantly larger than *A. flavipes leucogaster* for wt and hb in both sexes. *Antechinus minimus minimus* is significantly smaller than *A. flavipes leucogaster* in e for females (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. flavipes leucogaster* in absolute measurement for APV, IOW and I₁-P₃ for males and for APV and IOW for females. *Antechinus minimus minimus* is significantly larger than *A. flavipes leucogaster* in IBW, HT, PL, TC, NWR, HT-B, I¹-P³ and UPL for males and for IBW, HT, HT-B, I¹-P³, I₁-P₃ and UPL in females. *Antechinus minimus minimus* is smaller than *A. flavipes leucogaster* in absolute measurement for IPV, M²W, R-LM² and M₂W in females only. *Antechinus minimus minimus* is significantly smaller than *A. flavipes leucogaster* in IPV, M²W, R-LM¹, R-LM², R-LM³, BuL and

M₂W for males and for R-LM¹, R-LM³, SWR-LC¹B and BuL in females (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. flavipes leucogaster* occurs in south-west Western Australia. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. flavipes leucogaster* is 12.6-14.5%.

Antechinus minimus minimus versus
Antechinus flavipes rubeculus Van Dyck

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. flavipes rubeculus* has orange-reddish toned fur on the upper hind feet and tail base and a pale eyering.

External Measurements. *Antechinus minimus minimus* is significantly smaller than *A. flavipes rubeculus* in tv in both sexes (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. flavipes rubeculus* in absolute measurement for I₁-P₃ in males and for APV in females. *Antechinus minimus minimus* is significantly larger than *A. flavipes rubeculus* in APV, IOW, HT-B and UPL for males and for IOW, HT-B and I₁-P₃ in females. *Antechinus minimus minimus* is smaller than *A. flavipes rubeculus* in absolute measurement for IPV, M₂W, R-LC¹, R-LM¹, R-LM², SWR-LC¹B, BuL and M₂W in males and for IPV, M₂W, R-LC¹, R-LM¹T, R-LM², R-LM³, ZW, SWR-LC¹B, UML, BuL, UML and M₂W in females. *Antechinus minimus minimus* is significantly smaller than *A. flavipes rubeculus* in NW, OBW, R-LM¹T, R-LM³, ZW, UML and LML in males and for BL, Dent, NW, OBW, R-LM¹ and PL in females (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. flavipes rubeculus* is only found in the wet tropics of north-east Qld. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. flavipes rubeculus* is 15.1-16.3%.

Antechinus minimus minimus versus
Antechinus godmani (Thomas)

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. godmani* is more uniformly brown on the head and back with a naked-looking tail.

External Measurements. *Antechinus minimus minimus* is smaller than *A. godmani* in absolute measurement in tv for males. *Antechinus minimus minimus* is significantly smaller than *A. godmani* in hf and e in males and for wt, tv, hf and e in females (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. godmani* in absolute measurement for APV in females. *Antechinus minimus minimus* is significantly larger than *A. godmani* in APV for males. *Antechinus minimus minimus* is smaller than *A. godmani* in absolute measurement for IPV, M₂W, PL, TC, UML, LML and M₂W in males and for BL, Dent, IPV, M₂W, OBW, R-LM¹T, R-LM², R-LM³, ZW, PL, TC, UML, I¹-P³, I₁-P₃, LML, M₂W and UPL in females. *Antechinus minimus minimus* is significantly smaller than *A. godmani* in BL, Dent, IBW, OBW, R-LC¹, R-LM¹, R-LM¹T, R-LM², R-LM³, ZW, SWR-LC¹B, I¹-P³ and UPL in males and for IBW, R-LC¹, SWR-LC¹B, PML, BuL and I₁-P₃ in females (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. godmani* is only found in the wet tropics of north-east Qld. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. godmani* is 15.0-16.7%.

Antechinus minimus minimus versus
Antechinus leo Van Dyck

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. leo* is uniformly cinnamon on the head and back with slightly darkened hair forming a mid-dorsal head stripe.

External Measurements. *Antechinus minimus minimus* is smaller than *A. leo* in absolute measurement in tv for males and e in females. *Antechinus minimus minimus* is significantly smaller than *A. leo* in hf and e in males and for tv and hf in females (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. leo* in absolute measurement for IOW in males and for APV in females. *Antechinus minimus minimus* is significantly larger than *A. leo* in APV and I₁-P₃ for males and for IOW in females. *Antechinus minimus minimus* is smaller than *A. leo* in absolute measurement for M²W, NW, OBW, R-LC¹, R-LM¹T, R-LM², R-LM³, SWR-LC¹B, UML, BuL, LML and M₂W in males and for BL, Dent, IPV, M²W, OBW, R-LC¹, R-LM¹, R-LM¹T, R-LM², R-LM³, ZW, SWR-LC¹B, TC, PML, UML, BuL, LML and M₂W in females. *Antechinus minimus minimus* is significantly smaller than *A. leo* in BL, Dent, IBW, IPV, R-LM¹, ZW, PL, TC, NWR and PML in males and for IBW, NW and PL in females (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. leo* is known only from north of Princess Charlotte Bay, on Cape York Peninsula in far northern Qld. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. leo* is 13.4-15.1%.

Antechinus minimus minimus versus
Antechinus mysticus Baker,
Mutton and Van Dyck

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. mysticus* has a greyish-brown head and neck, merging gradually to yellowish-buff on the rump and flanks, with a buff-brown tail base and slightly darkened tip.

External Measurements. *Antechinus minimus minimus* is significantly larger than *A. mysticus* in wt, hb and hf for males and wt and hb in females. *Antechinus minimus minimus* is

significantly smaller than *A. mysticus* in tv for males and for e in females (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. mysticus* in absolute measurement for IOW, HT, HT-B and I₁-P₃ in males and for APV, IOW, HT, HT-B and I₁-P₃ in females. *Antechinus minimus minimus* is significantly larger than *A. mysticus* in APV, IBW, TC, I¹-P³ and UPL in males and for IBW, I¹-P³ and UPL in females. *Antechinus minimus minimus* is significantly smaller than *A. mysticus* in M²W, R-LC¹, R-LM³ and SWR-LC¹B in males and for M²W, R-LC¹, SWR-LC¹B and BuL in females (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. mysticus* occurs in scattered coastal populations between the Qld / NSW border in far south-east Qld and Eungella NP near Mackay in mid-east Qld. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. mysticus* is 14.5-15.2%.

Antechinus minimus minimus versus
Antechinus stuartii Macleay

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. stuartii* is more uniformly brownish-grey from head to rump.

External Measurements. *Antechinus minimus minimus* is larger than *A. stuartii* in absolute measurement hb in both sexes. *Antechinus minimus minimus* is significantly larger than *A. stuartii* in wt for both sexes and hf for males only (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. stuartii* in absolute measurement for APV, IOW and HT-B for males and for APV, IOW, HT, HT-B, I¹-P³, I₁-P₃ and UPL in females. *Antechinus minimus minimus* is significantly larger than *A. stuartii* in BL, Dent, IBW, HT, PL, NWR, I¹-P³, I₁-P₃ and UPL for males and for BL, Dent, IBW, PL and NWR in females. *Antechinus minimus minimus*

is significantly smaller than *A. stuartii* in M²W for females only and for M₂W in both sexes (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. stuartii* occurs only on mainland Australia, in eastern NSW north of about Sydney to far south-east Queensland (Girraween NP, Lamington NP, Main Range NP, Springbrook NP and Tamborine NP). Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. stuartii* is 12.1-14.9%.

Antechinus minimus minimus versus
Antechinus subtropicus
Van Dyck and Crowther

Pelage. *Antechinus minimus minimus* has coarse fur and a leaden grey head that merges to brownish yellow fur on the rump and flanks whereas *A. subtropicus* is more uniformly brownish from head to rump.

External Measurements. *Antechinus minimus minimus* is significantly larger than *A. subtropicus* in hb for females. *Antechinus minimus minimus* is significantly smaller than *A. subtropicus* in e for males only (Tables 1 and 8).

Craniodental Characters. *Antechinus minimus minimus* is larger than *A. subtropicus* in absolute measurement for IOW, IPV and I₁-P₃ for males and for IOW, IPV, HT and HT-B in females. *Antechinus minimus minimus* is significantly larger than *A. subtropicus* in IBW, HT, HT-B and I¹-P³ for males and for I₁-P₃ and UPL in females. *Antechinus minimus minimus* is smaller than *A. subtropicus* in absolute measurement for M²W and M₂W in females only. *Antechinus minimus minimus* is significantly smaller than *A. subtropicus* in M²W, PPV and M₂W for males and for PPV and SWR-LC¹B in females (Tables 1 and 8).

Comments. *Antechinus minimus minimus* occurs throughout most of Tasmania (including southern Bass Strait Islands) whereas *A. subtropicus* occurs only on mainland Australia, from far south-east Queensland north to just

north of Gympie in south-east Queensland. Genetics: uncorrected pairwise difference at the mitochondrial gene CytB between *A. minimus minimus* and *A. subtropicus* is 14.3-15.2%.

DISCUSSION

Systematics and Biogeography

The phylogenies reconstructed here (Figs 7-8) provide evidence of 15 putative species in the genus *Antechinus*. Species delimitations based on DNA work are necessarily arbitrary, depending on the strength of monophyletic clade support and relative depth/divergence of clades; all proposed antechinus species clades were distinctly clustered, deeply divergent (5-15% pairwise divergence at mtDNA), bearing strongly supported nodes (0.99-1.00 posterior probabilities).

Our DNA data corroborate the findings of Armstrong *et al.* (1998), who found similarly deep levels of divergence (using combined mtDNA and nDNA) among various antechinus species, including: *A. swainsonii*, *A. minimus*, *A. leo*, *A. bellus*, *A. godmani*, *A. flavipes*, *A. agilis* and *A. stuartii*. The present study provides a comparative genetic analysis that encompasses a range of recently resolved antechinus taxa that could not be included in the earlier work: *A. adustus*, *A. subtropicus*, *A. mysticus*, *A. argentus*, *A. arktos*, *A. swainsonii* (Tas), *A. vandycki* (Tas), *A. mimetes insulanus* (Grampians, Vic) and both *A. minimus minimus* (Tas and southern Bass Strait Islands) and *A. m. maritimus* (Victoria) from a range of geographic locations.

Our DNA evidence of species distinction within the genus *Antechinus* is consistently corroborated by a suite of other data sources, including: morphology (pelage colour, body size and craniodentary), biogeography (allopatric separation and/or relatively deep divergence across limited geographic distance) and/or ecology/behaviour (differences in breeding timing for a genus where breeding is known to be highly synchronised annually within any given species and asymmetrical between sympatric congeners.).

Assessing all comparative data, we conclude the total evidence strongly supports the existence of 15 species of antechinus, including a single species of Swamp Antechinus, *A. minimus*, that is appropriately characterised into two subspecies, *A. m. minimus* (Tas and southern Bass Strait Islands) and *A. m. maritimus* (Vic, SA, and nearby offshore islands).

The (direct sequencing) genetic work presented here broadly corroborates the (allozyme) genetic work of Smith (1983), who examined electrophoretic variation in *A. minimus* across Bass Strait. He concluded that given a mean genetic distance of 0.035 ± 0.009, the trans-Bassian populations of *A. minimus* warranted their subspecific status. Our genetic phylogenies suggest that *A. minimus* is distinctly different (monophyletic) with respect to all congeners; there were distinct but moderate genetic (3.9–4.5% at mtDNA) differences between subspecies and notable genetic divergence within each subspecies (*A. m. minimus* 0–1.2%; *A. m. maritimus* 0–1.8%). In our genetic phylogenies, *A. minimus* was positioned in a large clade, together with all four species in the Dusky Antechinus complex, to the exclusion of all other antechinus, indicating that these taxa have shared a common ancestor some time in the past (see also Baker, Mutton, Mason & Gray, 2015). The present subspecies status for *A. m. minimus* and *A. m. maritimus* would seem appropriate because comparatively, across Bass Strait, the subspecies of *A. minimus* (3.9–4.5%) are morphologically only subtly divergent for craniodental characters, where there are no significant differences (see below), and only about half as genetically divergent as recognised species pairs within the Dusky Antechinus complex that are found in Victoria (*A. mimetes*) and Tasmania (*A. swainsonii*) (9.4–11.6%), where there were numerous significant (and absolute) morphological differences (refer Baker, Mutton, Mason & Gray 2015). This relative pattern was also recovered by Smith (1983), who found that electrophoretic variation in *A. minimus* and *A. swainsonii* across Bass Strait differed markedly, with mean genetic distances of 0.035 ± 0.009 and 0.085 ± 0.015, respectively, prompting his suggestion at the time that subspecies status was

warranted in *A. minimus* and at least subspecies status was warranted for *A. swainsonii*.

The sampling of *A. minimus* in Smith's (1983) study included a couple of Tasmanian populations: Flinders Island (N=14) in the north and Bruny Island (N=13) in the south, compared to four populations on the mainland (Vic): Gembrook (N=1), Dartmoor (N=2), Cape Liptrap (N=7) and Cape Otway (N=10). Interestingly, Smith (1983) reported a mean genetic distance between the Flinders Island and Victorian *A. minimus* populations of 0.007 ± 0.010, whereas the mean distance between the Victorian and Bruny Island *A. minimus* populations was 0.037 ± 0.015; the genetic distance between Flinders Island and Bruny Island was 0.029. Thus, Smith concluded that the Flinders Island population was significantly closer genetically to the Victorian populations than to the Bruny Island population and he cautiously referred the Flinders Island *A. minimus* to the mainland *A. minimus maritimus*. Smith's view contrasted with Johnston and Sharman's (1977, 1979) referral of the Flinders Island populations of *Potorous tridactylus* and *Macropus rufogriseus* to their respective Tasmanian subspecies, and the prevailing view that the fauna of the Bass Strait islands are primarily Tasmanian (Hope 1973). In this regard, the results of the present study also contrast with that of Smith, because we sampled several Flinders Island *A. minimus* and also two individuals from Sth Bruny Island and found that they both claded strongly together with all other Tasmanian samples in our (mtDNA and nDNA) phylogenies to the exclusion of mainland *A. m. maritimus*. Interestingly, in our study the Flinders Island samples were slightly (1.2%) divergent to all other Tasmanian samples, except the sample from the Gardens in north-east Tasmania (closest to Flinders Island), to which they were 0.8% divergent. And yet all Tasmanian samples showed similar divergence to Victorian (mainland) samples: Flinders Island to Victorian samples (4.3–4.5% divergent) and all other Tasmanian samples to all Victorian samples (3.9–4.5%). The slightly greater mtDNA genetic difference of Flinders Island samples compared with all other Tasmanian samples (taken from both north and south Tasmania)

observed here may explain why Smith recovered some distinct allozyme differences between Flinders Island and Bruny Island samples, but cannot explain why he found a relatively closer connection between Flinders Island and Victorian samples, since our Flinders Island and Victorian Swamp Antechinus were relatively deeply divergent (4.3-4.5%). Interestingly, the single morphological (skull) specimen from Flinders Island available for inclusion in our analysis, MVIC C21965, is a very large male, that exceeds both *A. minimus minimus* and *A. minimus maritimus* in most length and width measures. This animal may be an example of the 'island effect' where small mammals may evolve rapidly towards larger size under reduced predation and competition (see Foster, 1964; Lomolino, 1985, 2005; Millien & Damuth 2004; Sondaar 1991; Van Valen 1973), which can accelerate morphological evolution in mammals, when compared to mainland conspecifics, by up to 3-fold (Millien 2006). Similarly, we found relatively larger skulls in *A. minimus minimus* from Maatsuyker Island (5.5 km off the south coast of Tasmania) compared to *A. minimus minimus* from mainland Tasmania.

Taken together, our results suggest that Flinders Island and Maatsuyker Island *A. minimus* should be regarded as *A. minimus minimus*, along with the rest of the Tasmanian *A. minimus minimus*. While no genetic samples could be obtained from Waterhouse Island, the supposed type locality of *A. minimus minimus*, it seems likely they would clade genetically with other Tasmanian *A. minimus*, since the geographic range between our Flinders Island and the Gardens samples encapsulates Waterhouse Island, with Flinders Island lying about 70 km to its north-east and the Gardens just 50 km to its south-east. We were unable to include a comparative genetic sample of *A. minimus* from King Island, which lies to the north-west of Tasmania; however, one voucher specimen we examined was from Martha Lavinia Beach on King Island, 39°39'S 144°04'E (QVM 1986.1.52). The crandiodental features of this specimen were consistent with Tasmanian *A. minimus minimus*, bearing large anterior palatal vacuities and narrower measures across

the snout and upper molar teeth, compared to mainland *A. minimus maritimus*. Thus, based on morphology of this specimen, King Island's geographic proximity (just 80 km off the Tasmanian north-west coast) and geological history (see below), it seems reasonable to assume these animals, like those on Flinders Island, are best considered *A. minimus minimus*. Recent work on the King Island Emu by Heupink *et al.* (2011) showed that models (Hope 1973; Lambeck & Chappell 2001) of sea level change indicate that Tasmania, including King and Flinders Islands, was isolated from the Australian mainland around 14,000 years ago. Up to several thousand years later, King Island (and presumably Flinders Island) was then separated from Tasmania. Heupink *et al.* suggested that initially a King Island/Tasmanian Emu population was isolated from the mainland taxon, after which the King Island and Tasmanian populations were separated. Our mtDNA results would suggest a similar evolutionary scenario for divergence initially between Tasmanian and mainland *A. minimus* (almost certainly predating physical continental separation) followed by Flinders Island (and likely King Island) *A. minimus* with Tasmanian *A. minimus*.

Antechinus minimus maritimus is also known from several neighboring islands off the south-east coast of Australia (Menkhorst & Seebeck 1999), including both Great Glennie Island and Kanowna Island, which are situated several kilometres off Wilson's Promontory (the southern tip of Victoria on mainland Australia); these islands have apparently been separated from mainland Australia for about 10,000 years (Wallis 1998) and the Swamp Antechinus found there have been purported as *A. m. maritimus* (Sale *et al.* 2006; Wainer 1976, 1978); we were unable to source genetic or morphological samples from either of these locations, but we assume them to be *A. m. maritimus* based on geographic proximity to the mainland and geological history; it would be interesting to see how genetically differentiated they are from Victorian populations of the subspecies.

Antechinus minimus is distinctly different in morphology compared with congeners. There

is sexual dimorphism for size, with males larger than females. Swamp Antechinus are leaden grey on the head and shoulders grading into rich yellowish brown on the rump and flanks; belly fur colour is greyish yellow or buff. The tail is short-haired, grizzled dark brown above, lighter below. The fur is coarse and grizzled; the foreclaws are long. The tail is short and the eyes and ears small. When compared with congeners, Swamp Antechinus are most similar, based on external body colouring (only), to *A. flavipes*. But *A. flavipes* have a marked pale eye ring, more orange-toned rump, fur on the feet and tail base, as well as a more marked darkened tail tip. The tail length is proportionately closer to head-body length in *A. flavipes*, compared with *A. minimus* and *A. minimus* is much more heavy-bodied than *A. flavipes*. In regard to their large body size, small ears and long claws on the forefeet, *A. minimus* are similar to members of the Dusky Antechinus complex.

Based on craniodental features, *A. minimus* is distinctive from every species of antechinus but most similar to members of the Dusky Antechinus complex, with large skulls bearing moderate-long palatal vacuities and long, well-spaced premolar rows. Our morphological analyses corroborate the DNA data in finding subtle craniodental differences between *A. m. minimus* and *A. m. maritimus*, where there were some size difference trends but none were significant. Specifically, *A. m. maritimus* tends to have a shorter tail and smaller feet than *A. m. minimus*. Also, *A. m. maritimus* tends to be larger than *A. m. minimus* for a range of craniodental features associated with breadth of the skull across the snout (R-LM¹T, R-LM², R-LM³), width of molar teeth (M²W, M₂W) and (to a lesser extent) length of molar row (UML, LML). These various size differences between *A. m. maritimus* and *A. m. minimus* are more pronounced in females than males, which is often the case in antechinus, because males vary more markedly in size range (both in overall body size and skulls) than females (see, for example, Baker, Mutton & Hines 2013; Baker, Mutton, Hines & Van Dyck, 2014; Baker, Mutton, Mason & Gray 2015; Baker, Mutton & Van Dyck 2012; Baker & Van Dyck 2012, 2013a,b).

Antechinus m. maritimus (Victoria) also tends to have smaller anterior palatal vacuities (APV) than *A. m. minimus* (Tasmania) (particularly in females). This morphological skull difference in APV is also notable in members of the Dusky Antechinus complex, which share similar biogeography and may co-occur with *A. minimus* on the mainland and Tasmania. Comparatively, in Tasmanian *A. swainsonii* and mainland *A. mimetes*, the former tend to have larger anterior palatal vacuities, together with narrower snouts and smaller molar teeth (Baker, Mutton, Mason & Gray 2015). The other Tasmanian Dusky Antechinus, *A. vandycki* from Tasman Peninsula, has even larger anterior palatal vacuities than *A. swainsonii* and is similarly less robust in skull breadth than the mainland *A. mimetes* (Baker, Mutton, Mason & Gray 2015). Such patterns of less robust skulls and longer anterior palatal vacuities in Tasmanian compared to mainland antechinus, while intriguing, are difficult to explain. Length of holes in the palate in fact varies among many species of dasyurid (Van Dyck, Gynther & Baker 2013). Archer (1981) speculated the size of palatal vacuities (and hypotympanic sinuses) in dunnarts (*Sminthopsis*) seemed, in general, to correlate with relative environmental aridity. This may relate to a rete-like exchange system at the interface between the narial and oral cavities via the soft tissue that spans the palatal cavities in the palatine, maxilla and premaxilla. Heat exchange was postulated to be involved, such that hot dry air breathed in by animals living in drier areas, would trigger increased evaporation within the oral cavity via the relatively larger palatal vacuities in the inland (more arid) species, which would in turn lower the temperature of the incoming air into the lungs, which itself in turn may result in less water being stripped out from the lungs on its way out. This interesting idea has never been formally tested, and it would probably be technologically difficult to do so (M. Archer, pers. comm.). In any case, such processes could not adequately explain the patterns observed here, since Tasmania tends to be both cooler and wetter than many mainland environments where *A. minimus maritimus* and *A. mimetes* occur, both of which exhibit the smaller incisive vacuities than their Tasmanian congeners (rather

than the larger maxillary/palatine vacuities observed in more arid-occurring *Smithopsis*).

Ecology

Antechinus minimus minimus

Distribution. *Antechinus minimus minimus* is widely distributed in wet sedgeland and swampy drainage areas mainly throughout western Tasmania, where it has been found at altitudes ranging from sea level to 1000 m (Green 1972). It occurs in habitats containing dominant species such as: button grass *Mesomelaena sphaerocephala* in association with *Calorophus lateriflorus*, *Restio australis* and *Lepidosperma filiforme*. Rainforest ecotonal and regrowth habitats occupied by *A. m. minimus* are characterised by *Ghania trifida*, *Sprengelia incarnata*, *Epacris gunnii*, *Monotoca* sp., *Boronia rhomboidea*, *Leptosperum* sp., *Gleichenia alpina*, *Casuarina dystyla*, *Eucalyptus gunnii* and *Poa caespitosa*. According to Green (1972), sphagnum moss bogs are also a preferred habitat. Green also notes that throughout its range, rainfall may average in excess of 250 cm p.a. and temperatures may vary from as low as -12°C in subalpine habitat to 35°C on the coast. *Antechinus m. minimus* may often be confined under snow drifts for weeks at a time.

Reproduction. Wakefield and Warneke (1963) and Green (1972) report a nipple number of six for *A. minimus minimus* (although one female held in the QVM confirmed by AMB had 8 young). Green (1972) reported a female with pouch young collected 6 December 1964 and suggested a breeding period from September to the end of December.

Little is known of diet or movement/range in *A. minimus minimus* populations. The status of this subspecies on Tasmania is regarded as secure because it occurs widely, and sometimes in apparent high density, across a range of habitats throughout much of Tasmania and the southern Bass Strait Islands.

Antechinus minimus maritimus

Distribution. Because of its affinity for dense wet heath, tussock grass and sedgeland *A.*

minimus maritimus occurs in a patchy, near-coastal distribution from south-eastern Victoria (Sunday Island) west to Robe in the south-eastern district of South Australia (Menkhorst 1995; Finlayson 1958). In Victoria, it may be found in both treeless vegetation and forests with a wet heath understorey (Wainer & Gibson 1976; Menkhorst & Beardsell, 1982) provided a dense ground cover is present for one or two metres above the ground. In south-western heaths, it has been found in areas that receive over 650 mm rainfall per year, where dominant species of vegetation included *Leptospermum myrsinoides*, *Xanthorrhoea minor*, *Banksia marginata*, *Melaleuca squarrosa*, *Sprengelia incarnata*, *Eucalyptus baxteri*, *Leptocarpon tenuax* and *Allocasuarina paludosa* (Menkhorst 1995; Menkhorst & Beardsell 1982). In south-eastern heaths (Great Glennie Island), upper stratum species included *Banksia marginata*, *Leptospermum laevigatum*, *Correa alba*, *Olearia phloggopappa* and *Myoporum insulare* with an understorey of *Poa poiformis* (Wainer 1976). *Antechinus minimus maritimus* is found in high density on the 60-ha Great Glennie Island, 6km west of Wilson's Promontory (the southern tip of Victoria) where it co-occurs with *Rattus fuscipes* (Wainer 1976, 1988) and also in high density on the 31-ha Kanowna Island, situated about 5km south-east of Great Glennie Island, where it is apparently the sole mammal species (Sale *et al.* 2006).

Reproduction. Ovulation and mating are synchronised but may occur a month later at Anglesea and Great Glennie Island than in the Wannon region (Wilson 1986). Earliest matings have been recorded in May and extend through to July. Young are born in July and August (Wilson 1986; Wilson & Bourne 1984; Wilson *et al.* 1990). All males succumb to a post-mating die-off, parturition occurs 28-32 days after mating and only a few females live through a second year. Females possess eight nipples (Wainer & Wilson 1995).

Diet. In one study, the diet of Swamp *Antechinus* on Kanowna Island was found to include a wide variety of prey. Remains of insect larvae, beetles, spiders, flies and ants were frequently

identified items in the scats of trapped animals; centipedes, scorpions, grasshoppers and lizards were also occasionally found to occur in Swamp Antechinus scats (Allison *et al.* 2006; Sale *et al.* 2006). Similarly, a wide variety of arthropods were found in the scats of individuals from a mainland population in the Otway Ranges, and on Great Glennie Island. This large variety of prey items would suggest *A. minimus* is a generalist species. The study on Kanowna Island found a high incidence of moth larvae in the *A. minimus* diet; moth larvae remains were found in about 95% of scats between August and October. Interestingly, even though this frequency of moth prey items fell in November and January, larvae were still the most important prey item in the diet, in terms of number, bulk and frequency (Sale *et al.* 2006; Wainer 1976, 1988).

Movements. In the eastern Otway Ranges of Victoria, the dispersal of nine litters of pouch young ($n = 62$) was assessed following two breeding seasons. Young males were found to remain on the natal site until December–January, dispersing before the breeding season. New males entered the population between January and June. More than 50% of females were residents at the study site and remained there to breed; the remaining females were trapped a single time. After the male die-off, movements of pregnant females increased, appearing to expand their home ranges. *Antechinus minimus* exhibits philopatry of females and dispersal of males, as observed in other *Antechinus* species. However, most antechinus disperse abruptly after weaning, whereas the Otways population of Swamp Antechinus were found to disperse 2–3 months after weaning (Magnusdottir *et al.* 2008).

Conservation. The preferred habitat of *A. minimus maritimus* is limited, so the Swamp Antechinus is patchily distributed and considered sensitive to human disturbance, particularly land clearance and urban development. *Antechinus minimus* prefers late successional vegetation; it is noteworthy that some populations were eliminated by bushfire in the eastern Otway Ranges, Victoria, and have unfortunately taken 20 years to re-establish (Wilson & Bachmann

2008; Wilson *et al.* 2001). Current threats to the species are habitat and population fragmentation, drainage of swamp habitat and frequent fire. Peak density of *A. minimus maritimus* in the eastern Otways area is 1–30 animals ha⁻¹. Comparatively, maximum densities at Walkerville in south Gippsland were estimated at 10 animals ha⁻¹. This in turn is in contrast to the islands off Wilsons Promontory, such as Great Glennie Island and Kanowna Island, where astonishing densities of 80 and 98 animals ha⁻¹, respectively, have been recorded. Such high densities on islands are well known among small mammals and have mainly been attributed to less interspecific competition and predation than is experienced by mainland populations (Gibson *et al.* 2004; Magnusdottir *et al.* 2008; Sale *et al.* 2006; Wilson & Bachmann 2008; Wilson *et al.* 2001).

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